EDITION REPORTS
G115
G7
V.31

DISCOVERY REPORTS

Vol. XXXI, pp. 123—298

Issued by the National Institute of Oceanography

LIBRARY
NOV 27 1961
FISH & WILDLIFE SERVICE

THE BENGUELA CURRENT

by

T. John Hart and Ronald I. Currie

CAMBRIDGE
AT THE UNIVERSITY PRESS
1960

Price seventy-five shillings net

PUBLISHED BY
THE SYNDICS OF THE CAMBRIDGE UNIVERSITY PRESS
Bentley House, 200 Euston Road, London, N.W. 1
American Branch: 32 East 57th Street, New York 22, N.Y.

Printed in Great Britain at the University Press, Cambridge
(Brooke Crutchley, University Printer)

[*Discovery Reports. Vol. XXXI, pp.* 123–298, *November* 1960.]

THE BENGUELA CURRENT

By

T. JOHN HART AND RONALD I. CURRIE

CONTENTS

INTRODUCTION . . . . . *page* 127

PREVIOUS WORK 130
Early voyages 130
Previous scientific observations 131
The work of the 'Meteor' Expedition 134

METHODS USED IN THE 'WILLIAM SCORESBY' 135
Observations and collections 135
Estimation of salinity and phosphates 137
Estimation of dissolved oxygen 137
Treatment of the plankton samples 139

ITINERARIES 141
Survey I (March) 141
Survey II (September–October) 142

COASTAL GEOGRAPHY AND BOTTOM TOPOGRAPHY 144

METEOROLOGY 147
Wind systems 147
The trade wind 147
The coastal winds 149
Weather preceding and during the surveys 150

SURFACE-CURRENTS 153
Previous data 153
Currents during the surveys 155

OBSERVED DISTRIBUTION OF TEMPERATURE AND SALINITY 156
First survey (autumn) 158
Horizontal distribution of temperature and salinity 158
Vertical distribution of temperature and salinity 161
Second survey (spring) 166
Horizontal distribution of temperature and salinity 166
Vertical distribution of temperature and salinity 169
Stability of the water masses 175

THE WATER MASSES 175
Water-masses of the South Atlantic 175
Temperature–salinity relationships of the South-west African waters . 177
Water masses of the upper layers (0–200 m.) 179
Oceanic and coastal surface-water 179
Dynamic height anomalies 179
Surface topography 181
Topography of the 200 db. surface 183
Water masses at 200–600 m. 183
The Antarctic Intermediate Water 184

UPWELLING 184
Previous work on the mechanism of upwelling 184
The effect of winds on the South-west African coast 185
Observed winds and hydrographical conditions 186
The mechanism of upwelling 188
Depths affected by upwelling 190
Centres of upwelling 191
Influence of the direction of the coastline 191
Seasonal variation of upwelling 191

NON-CONSERVATIVE PROPERTIES . . . . . *page* 192
The distribution of dissolved oxygen 192
Normal and abnormal conditions within the current 198
The distribution of dissolved inorganic phosphate-phosphorus . . 201

BOTTOM DEPOSITS 204

MICROPLANKTON 206
Terminology and presentation of data 206
Taxonomic notes 215
Diversity of the microplankton 219
Distribution of the main groups of microplankton 225
First survey 225
Second survey 229
Distribution of the main diatom groups 234
First survey 234
Second survey 240
Special distributional features 245
Observations on discoloured water 252
The distinction between offshore and inshore diatom floras . . . 256
The cosmopolitan distribution of marine plankton diatoms and the 'ecological characterization' of the more important species from the Benguela current 263

ZOOPLANKTON 268
Polychaeta 268
Chaetognatha 268
Entomostraca 268
Ostracoda 269
Mysidacea 269
Cumacea 270
Amphipoda 270
Euphausiacea 271
Decapoda and Stomatopoda 271
Mollusca 271
Larvacea 272
Eggs and young stages of fish 272
Distribution of the zooplankton 273

ECONOMIC RESOURCES OF THE BENGUELA CURRENT 274
Fish and fisheries 274
Seals 274
Whales 275
Guano Islands 275

REVIEW OF THE MAIN FEATURES OF THE BENGUELA CURRENT 277
Normal conditions 277
Abnormal conditions 278

COMPARISON OF THE BENGUELA CURRENT WITH OTHER UPWELLING REGIONS . 280

ORGANIC PRODUCTION IN THE BENGUELA CURRENT 284

SUMMARY 286

REFERENCES 289

THE BENGUELA CURRENT

By T. John Hart and Ronald I. Currie

(Text-figs. 1–96)

INTRODUCTION

When the National Institute of Oceanography took over the ships of the 'Discovery Investigations' in 1949 one of the first objects was to round off some of the work done in the southern hemisphere by the older organization. That research had included a survey of the Peru coastal current, carried out by the R.R.S. 'Willlam Scoresby' in 1931. The late E. R. Gunther, who was in charge of the scientific work at sea, published a valuable report on the results of that survey, which clearly demonstrated the need for further research in such areas. Other duties prevented further work on the data collected from the Peru current prior to the war, and since then much work has been done there by scientists from other countries. The smaller analogous region off South-west Africa on the other hand has received less attention. The 'William Scoresby', however, was recommissioned in 1950 for a voyage to South Africa and the Indian Ocean, and accordingly our new programme, planned in outline by Dr N. A. Mackintosh, allowed for a hydrological and plankton survey of the Benguela current, at first in February–March, and (after subsequent alterations to the ship's programme) again in September–October. There were thus two surveys, the first in the autumn and the second in the spring. They were carried out on similar lines, but within the limits imposed by other items in the programme, of which whale-marking was the most important.

In this report, which aims at providing a general interpretation of the observations made during these two surveys, we apply the name 'Benguela current' to the region of cool upwelled coastal water along the South-west coast of Africa. This water, characterized by a pronounced negative surface temperature anomaly is found mainly between 15° S. and 34° S., and within 100 sea-miles of the coast. Thus it forms only the eastern periphery of the anticyclonic gyral of the South Atlantic, and the adjacent circulation of warmer subtropical water to the westward is excluded. The latter we prefer to speak of as the South-east Trade Wind Drift.[1] This choice of nomenclature, avoiding the application of the name Benguela current to the whole northward flowing limb of the gyral, has arisen from evidence brought together both by Defant (1936) and in the present report, indicating that two distinct current systems are involved, very much as Gunther (1936*a*) found in the Peru current. Moreover, the name 'Benguela current' is very generally associated with the cold water, so that we hope our restriction of the use of this name to the coastal element will not be misleading, and that it may eventually become generally accepted.

The Benguela current, then, is one of those regions off the western coasts of the continents, where, through the action of the prevailing winds, the effect of the earth's rotation, etc., the cool, nutrient-rich subsurface waters well up to the surface. An intense production of phytoplankton throughout most of the year is promoted thereby, resulting in an abundance of marine life of all kinds.

The rich life of the sea in this region is in striking contrast to the desert or semi-desert conditions that prevail in the adjacent land areas. The cool water along the coast condenses the moisture from the sea-breezes blowing towards the land, in much the same way as if a mountain range intervened, and the coast lying to leeward, in the rain-shadow, as it were, becomes arid and desolate.

[1] Hydrographic Department, 1939.

The abundant marine life of the region contains much which is of value to mankind. Whales, fur-seals, guano islands and potentially rich fisheries are all to be found there. Linked up with these features are areas in the open sea along the coast, with extraordinarily low concentrations of oxygen in the subsurface layers; the bottom deposit of diatomaceous mud is devoid of all but a few highly specialized forms of life capable of existing under almost anaerobic conditions, for sulphuretted hydrogen is evolved through the action of sulphate-reducing bacteria, and locally, under conditions not yet fully understood, this process sometimes increases to such an extent that even the surface waters are affected (Copenhagen, 1934, 1953). This may prove to be one of the factors leading to the recurrent mass mortalities of fish, another peculiar feature usually encountered near the northern limits of the region. Later we shall refer to the lethal effect of oxygen deficiency but it can also reasonably be argued that these mortalities are due more directly to the action of noxious water-bloom, probably of dinoflagellates, since visible discolorations of the sea by super-abundance of living organisms are yet another phenomenon frequently met with, often coincidentally with the mortalities (Brongersma-Sanders, 1948). These mass mortalities and water-bloom formations, which usually take place between midsummer and autumn, seem to link up with seasonal fluctuations in the physical conditions; but the mortalities only assume catastrophic proportions at long intervals, and these show no regular periodicity. Possibly they may follow accentuated deviations from the normal variations in physical factors of the environment, for it will be realized that here again there is close analogy with conditions sometimes encountered off Northern Chile and Peru: the *aguaje* phenomena, the 'Callao painter' or 'el Pintor', and the dreaded 'el Nino' current.[1] Further data bearing on these problems were among our secondary objectives; primarily the surveys were planned to improve our knowledge of the current system as a whole—the norm against which more pronounced local and temporary deviations can be assessed.

Most of the earlier observations from the Benguela current formed but a small part of more extensive programmes as the ships concerned passed down the coast on their way to the Indian Ocean; and more recently, although four of the 'Meteor's' transatlantic profiles traversed the area, they were necessarily carried out at widely separated intervals of time, so that the extent to which they are comparable is limited. Dr Brongersma-Sanders, whose recent work provides an invaluable guide to the literature, has also emphasized the need for more data (1947), and pioneer South African workers in several different fields of research have done the same.

We endeavour to do full justice to previous workers in the next section of this report, but the point has been raised here to show that even such limited observations as could be carried out on a small ship over short periods could still be expected to further the knowledge of the region considerably.

The plan of the surveys consisted of three main lines of full 'stations' (off Walvis Bay, Sylvia Hill, and the Orange river) worked east and west, that is, nearly normal to the coast and to the main trend of the isotherms; and four lines of intermediate or subsidiary stations, the first in the northern part of the area east and west, the second south-westward out to the offshore end of the first line of full stations, and from the inshore end of each line of full stations to the offshore end of the next. The east and west lines were disposed almost on the same latitudes as the eastern portions of previous 'Meteor' profiles, and thus afforded some direct comparison with previous work. Positions of all the stations and the 200 m. depth contour are shown in Figs. 1, 2 and 4 (pp. 143 and 146).

During the first survey (Fig. 1), we endeavoured to work the outermost station on each east-west line in oceanic depths beyond the continental slope, and the spacing of subsequent stations was therefore determined partly by the width of the shelf in the longitudes chosen and partly by practical

[1] Hitherto known by this name in oceanographical literature, Schweigger (1949) has recently challenged the correctness of this usage.

considerations. In general they were from 10–25 sea-miles apart. At full stations complete series of water-samples with temperature determinations at standard depths throughout the water-column were obtained; simultaneously standard series of vertical-closing plankton nets were fished down to 1000 m., or as deep as soundings permitted, and a vertical haul with the fine-meshed phytoplankton net was made. Towed plankton nets were not fished during the first survey owing to lack of time. Full details are given in the Station list (see references).

At the intermediate stations the ship was hove-to for a vertical haul with the phytoplankton net, which enabled us to make temperature observations with the bathythermograph loaned by the U.S. Navy, down to the limit of the depth range of the instrument (138 m.). Three hauls with a commercial otter-trawl (WS 974, 990, 999) were made on the continental shelf, providing some indication of the nature of the demersal fish-fauna and material for speciation studies in the genus *Merluccius* (hake) by Mr N. B. Marshall of the British Museum (Natural History).

Seventeen full stations and twenty-two intermediate stations were worked, over the area of some 60,000 square miles, in nine days. We could not spend more time in order to make the coverage more complete, since this could only have been done at the expense of the rest of the ship's programme. Details of the itinerary are given below (pp. 141–144).

The second survey (Fig. 2) was essentially a repetition of the first, at the opposite season of the year, but with more time available it became possible to increase the collections at the reoccupied stations, and to make some additional observations. Oblique and horizontal towed plankton-nets were fished at all full stations in addition to the vertical series, and horizontal towed nets at intermediate stations. Bottom samples were collected at nearly all the stations on the shelf, and a few additional stations were occupied for this purpose alone, to gain further knowledge of the distribution of the diatomaceous 'azoic' mud. The ship also worked in collaboration with Commander W. J. Copenhagen for a brief period while in the Walvis Bay area, assisting in researches he has described in another report (Copenhagen, 1953). Additional intermediate stations were worked both north and south of the area previously covered, and alternate stations on the most northerly, east–west line were made into full stations. Thus the number of full stations was increased to twenty and of intermediate stations to forty-four (thirteen being bottom-sampling stations only).

Full details of meteorological, physical and chemical data collected, and biological collecting gear used at each station on both surveys, are given in the Station List, already published in the Discovery Reports (1953). Methods are described and discussed in a later section of this report.

The ship was commanded by Lieut.-Cmdr A. F. Macfie, O.B.E., R.D., R.N.R., whose experience and ready assistance with the work at sea, and advice to the scientists when practical considerations rendered modifications of programme unavoidable, were prime factors in the successful completion of both surveys. Mr R. Baty, the chief Engineer, and his department gave unstinted help in servicing scientific gear, despite unlooked for difficulties with other auxiliary machinery. Mr K. Maclean, the chief officer, who organized the assistance needed from the watch on deck during station work, also obtained valuable recorder runs with the echo-sounding machine, and with the bo'sun, Mr Yorke, devoted much care to its maintenance. Mr M. R. B. Hawkins, the navigator, also recorded meteorological data, and Mr W. Slater, third officer and trawling expert, also helped in many ways outside his routine duties. Such projects must always depend upon the able co-operation of the whole ship's company, so that the data recorded and the biological collections made are a reflection of the way all hands turned to at an arduous, unfamiliar assignment.

The scientific personnel were Dr T. J. Hart, Dr (then Mr) Robert Clarke and Mr R. I. Currie. Dr Hart was in charge of the work at sea during the first survey, handing over to Dr Clarke at the Cape

as previously arranged. Dr Clarke's judgement in making additional observations during the second survey, when more time unexpectedly became available, greatly increased its value. Owing to his preoccupation with whaling research he has not participated directly in the writing of this report. In preparing the account of the second survey we have frequently made use of his journal. That the field work owed much to his efforts throughout should be obvious. All chemical estimations made at sea were carried out by Mr Currie.

We are particularly indebted to the Director of the Marine Biological Association's Plymouth Laboratory and his staff for unrivalled working facilities before the new premises of the National Institute were available, for much fruitful discussion and for practical help. By arrangement with Dr G. A. Steven, Skipper W. H. Crease with his crew of the R.V. 'Sula', and the M.B. 'Gammarus', gave much help while the ship was in Plymouth on her outward voyage, and again on her return.

All our colleagues on the staff of the National Institute have assisted the work in some measure, but special thanks are due to Dr G. E. R. Deacon and Dr N. A. Mackintosh for their valuable advice and encouragement during the preparation of this report, to Dr H. F. P. Herdman for the care and attention he devoted to the scientific equipment of the ship before sailing, and to Miss D. M. E. Wilson for assistance in computing of values and checking data for the station list.

The assistance of the naval authorities who 'mothered' the ship when she called at Devonport, Gibraltar, Freetown and Simonstown, extended down to the provision of odd spares for what must have seemed to them some very odd gear, and was, of course, absolutely essential to the successful completion of this part of the programme.

We also wish to record our thanks to the Director of the Naval Weather Bureau for providing relevant meteorological data; to Cmdr C. E. N. Frankcom, O.B.E., R.N.R., of the Marine Division, Meteorological Office, and to Mr E. W. Barlow of his staff for data on surface drift and much helpful discussion.

Dr J. H. Oliver assisted greatly in devising a suitably robust instrument for carrying out our phosphate determinations and by providing laboratory facilities in London before the ship sailed. Dr K. R. Butlin, of D.S.I.R., assisted by confirming the presence of sulphate-reducing bacteria in the bottom-sample from St. WS 1074.

Many people in the Union of South Africa befriended the ship, both officially and personally. Among those who helped more particularly with our Benguela current problems were: Dr C. von Bonde, then Director of the Fisheries Survey Division, Department of Commerce and Industries, and his staff, who gave us laboratory facilities and opportunities for discussion on many topics of common interest. The Head of the South African Weather Bureau provided most valuable data. Commander W. J. Copenhagen, with whom we have discussed plankton production and the 'Walvis Bay problem' over many years, introduced us to Dr Liebrandt, Director of Chemical Services, Department of Agriculture, who provided chemical laboratory facilities on this occasion. Dr S. P. Jackson of the Geography Department, University of Witwatersrand, gave most valuable advice on the meteorological factors involved, as did Professor J. H. Day of Cape Town University on zoological matters. Dr J. H. Maconnell of Walvis Bay, supplied some first-hand local information on the fish mortalities.

PREVIOUS WORK

Early voyages

West African exploration received its greatest initial impetus in the latter half of the fifteenth century. Continuing their pursuit of the Moors, the Portuguese initiated a series of somewhat warlike exploratory voyages down the West African coast. Attempts to sail southward were for a long time

defeated by a great reef off Cape Bojador, but this was eventually passed in 1433 or 1434, and further voyages became more and more directed towards trading and colonization. King John commissioned an esquire of his country, Diego Cao, to continue further exploration into the Gulf of Guinea, and on his second voyage in 1484–6 Diego Cao penetrated southward beyond the mouth of the river Congo (Ravenstein, 1900).

It was the custom of the Portuguese at this time to set up marble pillars surmounted by a cross, with which to mark their achievements. These pillars, or 'padraos', had been introduced to replace wooden crosses which were used before but found to rot away too quickly. Diego Cao carried several of those padraos with him, constructed and suitably inscribed, before leaving Portugal. He set up one at the most southerly point which he reached, naming it 'Cabos do Padraos'. It is now known as Cape Cross. It seems that Cao sailed rather further south than this, to about 22° 09′ S., before he returned to the north.

Interesting to note is a remark by Ravenstein (1900) on Martellus's chart, which documented the discoveries of this period. He says, 'To the south of it [Cape Cross] on Martellus' chart, we notice a Praia dos Sardinhas (sardine shore), now known as Sierra Bay...'. The position of this shore coincides with the region where we now know that extensive mortalities of fish occur. It is possible, therefore, that Diego Cao had observed such a mortality of sardines.

Diego Cao appears to have died on the return voyage, and the exploratory work was taken over by Bartholomeu Diaz. Diaz left Portugal in 1487 and was the first to succeed in rounding the Cape of Good Hope. He set up a padrao at Luderitz Bay (Diaz Point) and another at the Cape. The final linking up of the trade route to the east was accomplished by Vasco da Gama (1497–9) (Ravenstein, 1898). One might conjecture that da Gama had benefited from the experience of his predecessors for on his way to the Cape he stood well out to sea and first touched the South African coast at St Helena Bay. In so doing he would have avoided the greater part of the contrary currents and winds of this coast, and would have been able to tack into the trade wind, but there is, of course, no proof that it was these considerations that led him to adopt such a route.

Although the early Portuguese place-names are very descriptive and tell us a lot about their observations, no detailed records of these voyages have been found. Several expeditions visited this coast in the following centuries, principally in search of guano and further inland exploration, but not until the nineteenth century have we been able to find any records of meteorological and hydrographical observations.

Previous scientific observations

In 1820 Major James Rennell summed up the existing knowledge of the ocean currents' and this work was published posthumously in 1832. With regard to the currents of the South-west African coast he remarks (pp. 119 *et seq.*):

> But we have no detailed accounts of the circumstances of the currents along-shore, between the parallels of 28° and 11½° south, although the existence of such is well known; so that the continuity of the thread of current is never broken between that in the Indian Sea and the Equatorial current. The first notice, from authority, of a current hereabout, is its issuing from the deep recess of the coast of Benguela, between 9½° and 11° S., in a W.N.W. and N.W. by W. direction, (as if the water had been forced in there) and with a rate of 14 to 25 and 30 miles per day.
>
> From the just mentioned Bay of Benguela the current ranges along the coast to the N.W. receiving the waters of the Zahir or Congo River, the outfall of whose waters runs nearly in the same direction with the sea current, that is N.W., and only marks its character by the increased velocity of the stream, and the lowering of its temperature.

While commenting thus on the coastal currents, Rennell was well aware of the more definite drift produced by the trade wind farther from the coast. This he called the South Atlantic current.

The generally accepted theory that the cold current along the coast was a direct flow from high southern latitudes was held until the middle of the nineteenth century, although Rennell recognized a continuity in the surface drift from the Indian Ocean to the Atlantic, around the Cape of Good Hope. Sir James Clark Ross (1847) on his passage to the Antarctic carried out a series of temperature measurements around the Cape, which show conclusively that the cold water on the west coast was an isolated phenomenon, and was not continuous to the south. Whilst approaching the African Coast in the vicinity of Paternoster Point on the 8 March 1840, he remarks:

By 1 p.m. the next day the temperature of the sea had fallen from 70° to 56·5° F., that of the air being 65° and the mist unpleasantly cold to our feelings. We were at this time in 32° 21′ S., 17° 06′ E., therefore about 45 miles from Paternoster Point, when we struck soundings in 127 fathoms on a bed of fine dark sand. We had expected to have found an elevation in the temperature both of the air and sea on our approach to the African coast, by reason of the heat radiation from its shores; but the cause of the depression became evident on the morning of the 9th, when having sighted Cape Paternoster at daylight, we found we had to contend against a current increasing in strength and coldness of temperature as we neared the land.

Ross had to spend several days beating up to the Cape, and while doing so he took the opportunity of making observations of temperature at different depths and distances from the land. These he has tabulated, and from them he concludes:

All these circumstances combine to show that a northerly current of very limited extent, but of considerable force exists from the Cape of Good Hope, along the western coast of Africa; which in general terms, may be represented by a volume of water sixty miles wide and two hundred fathoms deep, averaging a velocity of one mile per hour, and of the mean temperature of the ocean, running between the shores of Africa and the waters of the adjacent sea. The cloud of mist which hangs over this stream of cold water is occasioned, of course, by the condensation of the vapour of the superincumbent atmosphere, whose temperature is generally so many degrees higher than that of the sea. It is sufficiently well defined to afford useful notice to seamen of their near approach to the land.

After leaving Simon's Town, Ross continued his temperature measurements, and

found the temperature of the surface of the sea to increase rapidly after leaving Cape Point,... showing that we had got to the southward of the cold water current that runs along the west and perhaps the south coast of Africa.

It is evident therefore that this current does not come down directly from the south, as it only extends to seven or eight miles from the Cape and beyond that distance we have to descend to over six hundred fathoms to find water of so low a temperature.

These observations do not appear to have received very wide attention, for even up to 1910 (Engeler), some authors upheld the continuity between the West Wind Drift and the cold current on the west coast of South Africa. Findlay (1874), Bourke (1878) and Galton (1883) all speak of a south polar current on this coast, although Bourke appears to have been mystified by the patchy distribution of the cold water. 'But the most remarkable feature of this N.W. current from the Cape of Good Hope is the sudden manner in which its cold waters simultaneously appear along the land to the northward of Cape Frio.'

The origin of the cool water by upwelling was inferred both theoretically and by comparison with other regions by Witte (1880), Buchan (1895) and Schott (1902). It was finally confirmed by the serial oceanographical observations of S. M. S. 'Möwe' (Schott, Schulz and Perlewitz, 1914).

Many early writers on the region make general references to its great wealth of marine life. Pechuël-Loesche (1882, p. 283) writes of 'a species of herring *Pellona africana* that presses shorewards from the South Atlantic current in immense shoals, from November to February'. Though most of his observations were made far to the north, where the upwelling is a much more seasonal phenomenon than in the region off South-west Africa, the analogy with the behaviour of other clupeoids farther south is most striking. Pechuël-Loesche also appears to be responsible for the present name of the current.

As we have said, Rennell (1832) applied the name 'South Atlantic current' to the more definite drift of the trade wind offshore. Later, Findlay (1867) called the current the 'South African current', a name also used by Dankleman (1878). This name referred to the whole water movement off the west coast of South Africa, and this again was termed the 'Sud-atlantische Strömung' by Pechuël-Loesche (1882). In a later paper, however, cited by Schott (1931), Pechuël-Loesche uses the name 'Benguela-strömung'. The *Africa Pilot*, Part II, 1939, distinguishes two current systems, the South-east Trade Wind Drift, and the Benguela current inshore, and as stated previously we have chosen to follow this nomenclature throughout this paper.

Of the more recent expeditions to the South-west African region, that of the *Valdivia* has contributed most to our knowledge of the biology of the region. The majority of their stations lay further from the coast than we could have wished, but nevertheless their observations have helped to lay a basis for later work. In collating these observations Schott (1902) was able to summarize the existing data on the physical phenomena of the region, but of all the 'Valdivia's' work that part which has been of most service to our present investigations is the great advance in the taxonomy of many of the southern subtropical organisms which resulted from her collections in adjacent waters. Karsten's report on the phytoplankton (1906), which quotes from Schimper's field notes, has been a constant help in working up the microplankton.

The voyage of S.M.S. 'Möwe' in 1911 was more strictly concerned with surveying the coastal regions, and some valuable physical and chemical data were collected. Evidently no biological observations were made. The physical data have been dealt with by Schott, Schultz and Perlewitz (1914) and later by Franz (1920, 1921) who considered at length the seasonal fluctuations of the current.

Our knowledge hitherto of the oceanographical phenomena of the region is, however, based principally on the extensive work of the Deutsche Atlantische Expedition 'Meteor'. The data collected by the 'Meteor' enabled Defant (1936) to investigate the mechanism of the current system, while numerous papers, among which Hentschel's work is outstanding, have provided an understanding of the general biology of the region. The 'Meteor's' work will be referred to later (p. 134).

Systematic collecting by the vessels of the Discovery Committee, which in these waters was mostly during the winter months and off the southern part of the South-west African coast, has aided the identification of our material, and has also been a guide to the extent to which species found in abundance in the Benguela current are peculiar to that region, or are merely local concentrations of wide-ranging oceanic forms. In this way both Hendey's report (1937) on the Plankton Diatoms of the Southern Seas, and John's report (1936) on the southern species of the genus *Euphausia*, help in the interpretation of the 'William Scoresby's' collections.

Much pioneer work has been carried out by the South African Division of Fisheries and Marine Biological Survey under the direction of Dr J. C. F. Gilchrist and latterly by Dr C. von Bonde and his successors. Dr K. H. Barnard of the South African Museum has been particularly active among the many specialists working upon this material, and although the collections rarely extended north of the Orange river, they form the basis of our knowledge of many species extending farther north. Boden's account (1950) of the coastal plankton diatoms from Cape Peninsula to Lambert's Bay has been a constant help.

Work on analogous conditions elsewhere has, of course, advanced our knowledge of the basic physical and biological factors important in upwelling regions. Schott's work (1902, 1931, 1942, 1951) on the Peru current and upwelling regions generally, has done much to show how closely analogous the different upwelling regions are. Gunther's account (1936) of the work of the 'William Scoresby' in the Peru current, gives details of the current pattern, mortality phenomena and discoloration of the sea, all of which are closely mirrored in the Benguela data.

Perhaps the best known of all upwelling regions, owing to its ready accessibility, is the Californian current. Abundant recent researches into its oceanography carried out by various leading workers show essentially similar relationships to those which we have found in the Benguela current. The numerous references in later sections should show how valuable this work has been in interpreting the present data.

One feature of the Benguela current region which has attracted widespread interest is the occurrence of fish mortalities, particularly in the vicinity of Walvis Bay, and their possible causes, biological or otherwise. The whole subject has been comprehensively discussed by Dr Brongersma-Sanders (1948) who treats all the relevant literature thoroughly. This and further recent work, in particular some of the results of the Danish 'Galathea' Expedition (1950–2), will be discussed in the appropriate sections.

The work of the 'Meteor' expedition

The extensive data collected by the 'Meteor' in 1925–7 have revealed the general pattern of the circulation in the South Atlantic (Wüst, 1950) and the disposition of the observations was such that some of them fell within the South-west African region. This enabled Defant (1936) to present the most complete account of the region so far.

The 'Meteor' observations consisted of several more or less latitudinal lines of stations across the Atlantic Ocean. The eastern ends of five of those great sections fell within the Benguela current, and it is those stations which Defant used. Defant supplemented his study of the 'Meteor' observations by a new analysis of the Dutch surface current observations. These he meaned in one degree areas (one degree of latitude by one degree of longitude) for each quarter of the year, and his results (Fig. 6) present us with an interesting new interpretation of the surface water-movements. The outstanding feature of these current charts is that they reveal a one-sided line of divergence. It lies in a N.N.W. direction along the coast, from about 20° to 30° S. In the south it is about 160 sea-miles from the coast, and in the north 300–350 sea-miles. To the west of this line the current sets to the west, but to the east of it the current runs more or less parallel to the divergence but is somewhat irregular on its coastal boundary.

Comparing this system with the iso-anomaly lines of surface temperature (the lines of equal difference from the latitudinal mean) Defant further finds that the region of strongest negative anomaly, the coldest water, is confined to the coastal current, and is most marked in the region between 23° and 31° S. where the divergence is also most pronounced.

The vertical thermo-haline distribution on the five 'Meteor' 'Profils' shows a correspondingly good agreement with the surface picture. 'Profil' IV in 34° S. shows but little evidence of upwelling close against the land, while on 'Profils' II (28½° S.) and VII (22° S.) the characteristic uplift of the isotherms and isohalines against the coast indicates the upwelling of the subsurface-waters from a depth of about 300 m. The more northerly 'profils' suggest a sinking rather than an uplift of water against the coast. In 'Profil' VI (15–16° S.) the isotherms and isohalines, at a depth of 30–40 m., descend toward the coast, and in 'Profil' VIII (9° S.) this is even more pronounced. Thus the region of most intense upwelling, as adduced from the vertical pictures, corresponds with the position of the most marked negative surface temperature anomaly and the most well-defined divergence in the surface currents.

Defant then considers theoretically the problem of the circulation by examining the effect of winds on two bodies of water of different density lying in a canal. This will be discussed in more detail later, but for the present it will suffice to say that by applying his derived theory to the South-west African waters, he concludes that outside the divergence there must be a vertical eddy in the upper layers. Below the axis of this eddy the water will move towards the east, ascending to the surface inside the

divergence line and producing in the coastal waters a distribution of density such that a current will form parallel to the coast. Seawards of the divergence line, and in the upper part of the vertical eddy, the water will be transported offshore.

Studying the general biology of the region, Hentschel (1936) found it necessary to adopt some arbitrary spatial definitions of the several sea areas he discussed. The 'ten degree field' extending westwards as far as St Helena which he took as his Benguela current region has unfortunately masked the great richness of the coastal current inshore. Consequently most of the generalizations he felt able to make apply rather to the subtropical oceanic surface water. Of the existence of the rich coastal belt he was, of course, very well aware. This was the only part of the region where large quantities of diatoms were to be found among the microplankton. He did not, however, regard the coastal current as distinct from the oceanic circulation, whereas our present results indicate that the natural boundary between the two types of surface-water is more significant than any of the boundaries of his arbitrarily chosen areas. No doubt he was unable to demonstrate the effect of this natural boundary on account of the wide spacing of the 'Meteor' stations, and the fact that the physical data were only partly digested by the time his work was published. His reference to the characterization of the region by the steep east–west gradient in microplankton quantities rather than by an abrupt transition such as our results indicate, his inclusion of many warm-water forms among the characteristic dominants of the region, and his insistence on the dominance of Dinophyceae over Diatoms among the protophyta, all arise from the same causes. Provided this is all borne in mind it can be seen that his generalizations are in very good agreement with our own findings—that is, apart from his insistence on the importance of the 'South-west Africa Tongue' which will be discussed later.

While extremely valuable for interpreting the large-scale picture, the 'Meteor's' observations unavoidably had the disadvantage of being widely spaced both in time and geographically, and the 'William Scoresby' surveys can be considered as the next logical step in making a more localized and intensive study of the Benguela region in particular.

METHODS USED IN THE 'WILLIAM SCORESBY'

Observations and collections

Throughout the two surveys the watch-keeping officers maintained regular meteorological observations. In addition to those kept at four-hourly intervals, further records were taken while the ship was occupied on 'station'. The observations included personal estimates of the force and direction of wind, sea and swell, and instrumental records of barometric height, and dry- and wet-bulb temperature.

Continuous echo-soundings were made whenever possible, but these were restricted to the continental shelf and slope, as the depth range of the machine (720 fathoms, 1317 m.) did not permit any deep-water sounding. The latter were eventually obtained by a Lucas wire-sounding machine, but unfortunately this was not functional during the first survey. On the second survey, however, the Lucas machine made it possible not only to obtain deep soundings but also to delimit the extent of a region of reducing mud on the sea floor. For this the sampling technique depended upon the nature of the sediment, and both Baillie rods and snapper leads were found effective. The samples were preserved in alcohol after a preliminary examination.

The 'William Scoresby' was fitted with a distant-reading thermograph which provided a continuous record of the sea temperature. Since the bulb of this instrument was installed in the engine condenser intake, the record represents the temperature at a depth of about 4 m., but this of course varied considerably with the degree of loading of the ship. Checks on the accuracy of the instrument

were made frequently by comparison with insulating water-bottle measurements, and showed no significant deviation from the original calibration.

It was decided while planning the surveys that intermediate observations of temperature between the lines of full stations would be invaluable in constructing a detailed picture of the upper layer circulation. For this a bathythermograph was used. The instrument, the standard U.S. Navy pattern manufactured by Wallace and Tiernan Prod. Inc., New Jersey, conformed to the specifications of accuracy prescribed by the makers. (Temperature $\pm 0{\cdot}1^\circ$ F. and pressure $\pm 4\frac{1}{2}$ ft. with a depth limit of 450 ft.) Frequent calibrations of both temperature and pressure elements indicated a remarkable constancy, and no correction of the results has been necessary.

All water-samples were taken by standard methods, at the depths recommended by the Association Internationale d'Océanographie Physique. The Nansen–Pettersson insulating water-bottle was used for sampling the shallower depths, as a rule not over 400 m., but on certain occasions it was operated to a depth of 600 m. when an additional reversing hoist could be omitted thereby. At greater depths Munro-Ekman reversing water-bottles were employed. Three of the latter were used in each hoist, and while all carried two protected reversing thermometers, the upper and lower bottles were equipped with unprotected reversing thermometers as well.

Biological collecting during the surveys was mainly confined to standard series of plankton net hauls. The nets used and method of fishing were similar to those employed during the pre-war work of the Discovery Investigations (Kemp, Hardy and Mackintosh, 1929). The vertical series at full stations in oceanic waters included hauls with the Nansen pattern closing net, 70 cm. diameter at the mouth (N 70 V), at depth intervals of 50–0 m., 100–50, 250–100, 500–250, 750–500 and 1000–750 m. At shallow water stations the series was modified so as to work as close to the bottom as possible. A 100–0 m. vertical haul with the N 50 V phytoplankton net was also made. During the second survey oblique hauls were made with the 1-m. stramin net (N 100 B) and 70 cm. silk tow-net (N 70 B) on 200 m. of warp, maximum depth being recorded by Kelvin tube, and a 1-m. net (N 100 H) was also towed horizontally at the same time. These were in addition to the vertical series. Towed nets were not used during the first survey. In addition to the hauls at full stations, the N 50 V was worked at all the intermediate bathythermograph stations on both surveys.

A full-sized commercial otter-trawl (OTC) and conical dredge (DC) were used at a few stations on the shelf during the first survey, and during the second, numerous bottom-samples were collected with snapper-lead and Baillie rod. Full details of dates, times, etc., at which these types of gear were used are given in the Station List (1953) which also includes full definitions of the standard abbreviations employed.

The centrifuging of water-samples was not employed as a routine method for phytoplankton sampling, but was used for provisional identifications of dominant organisms in areas of discoloured water, whence surface-samples were preserved for subsequent analysis.

It was important above all to extend the basic physical and chemical observations over the widest possible area, and it was mainly for this reason that we did not attempt more comprehensive work on the phytoplankton, and more particularly on the smaller organisms known to escape nets. The Harvey method of pigment extraction from the catch of a fine-meshed vertical net fitted with a flow-meter (Harvey, 1934), which had proved most useful in the antarctic zone (Hart, 1942) was not used because it was already known from the 'Meteor' results (Hentschel, 1936) first, that dinoflagellates were of vastly greater relative importance in this area than in the antarctic, and their mixed pigments tend to vitiate direct visual colour match; secondly, that the nanno-plankton forms would similarly be of greater relative importance here. In the event, we found diatoms so numerous in the rich coastal belt that the earlier form of Harvey's method would most certainly have yielded valuable results. More

recent refinements of the pigment extraction method successively developed by Riley (1938), Krey (1939) and Richards and Thompson (1952), should certainly prove a most valuable line of investigation in the Benguela current area.

Estimation of salinity and phosphorus

The confined laboratory accommodation on board the 'William Scoresby' made it necessary to restrict as much as possible the amount of analysis carried out in the ship. Estimations of at least salinity, phosphate and oxygen were desirable for the work. Of these properties the salinity is by far the most stable, and unaffected by normal storage, and it was decided to keep the salinity samples for later analysis on shore. This has been the practice in the past on board the 'William Scoresby'. The estimations were eventually made by the Government Laboratory, London, to whom we owe our thanks.

The Atkins–Denigès colorimetric method was used for the determination of the dissolved inorganic phosphate-phosphorus. Recently, many new photometric systems have been described, which facilitate the colour comparison and attain a high standard of accuracy, but after experimentation both before the cruise and later on board the ship, it was decided that in the conditions in which we worked a visual comparison would yield the most satisfactory results of the required degree of accuracy. This method was adopted and we are greatly indebted to Dr J. H. Oliver for perfecting a suitable instrument for the purpose.

A Lovibond type of colorimeter was used. This had a series of thirty-three specially made glass slides, with colours flashed on to them representing a range in phosphate concentration from 0·03 to 3·00 mg. atoms P/m.^{3} The slides were calibrated by the same operator in a shore laboratory, against standard phosphate solutions (KH_2PO_4) made up in phosphate-free sea-water. (This latter, of salinity 35·00‰, was collected for the purpose in the Gulf of Guinea.) This procedure obviated any salt-error in the estimation. The sensitivity of the method varies slightly with the intensity of colour, and is at its lowest, $\pm$0·05 mg. atoms P/m.^{3}, at concentrations of 3·00 mg. atoms P/m.^{3} All the phosphate samples were analysed within a maximum of 10 hr. after collection.

Estimation of dissolved oxygen

Winkler's method was used for the determination of dissolved oxygen. The samples were stored under a water-seal in the precipitated form ($Mn(OH)_3$) and all were analysed within 20 hr. of collection. Standardization of the sodium thiosulphate was effected by titration with an approximately equal strength (0·22 N) solution of potassium iodate. This standard, kept in a slightly alkaline solution, proved very stable even in the most adverse climatic conditions.

For normal sea-waters the Winkler method works very well, but in the presence of certain contaminants the analysis can lead to erroneous results. It was to be expected, therefore, that in the vicinity of the South-west African coast, where organic production is very high, such contamination might be encountered. The principal sources of interference were considered to fall into three groups:

1. Large quantities of micro-organisms in the samples.
2. Relatively high concentrations of nitrites.
3. The presence of hydrogen sulphide.

Organic matter can affect the Winkler estimation in two ways. First, direct oxidation of organic matter is very rapid around pH 12·0, and this might occur during the initial alkaline stage of the analysis. Secondly, the iodine when liberated is liable to be absorbed by the micro-organisms. As it was not possible to analyse all the samples immediately after collection, and as they would have to be stored in one or other of these two stages, it was necessary to decide which course would cause the

least interference. Experiments on the determination of oxygen in dilute dinoflagellate cultures were made at the Marine Biological Association's Laboratory at Plymouth before the cruise. Those demonstrated that the principal interference took place through absorption of iodine by the dinoflagellates. Samples titrated immediately after acidification and liberation of the iodine showed a higher oxygen content than those titrated 2 hr. after acidification. In this period the mean absorption of iodine was equivalent to 0·4 ml. of oxygen per litre at 15° C. in 3 hr. No difference was observed in samples stored in alkaline-precipitated condition for periods up to 10 hr. It was decided, therefore, to store samples in the latter condition.

Allee and Oesting (1934) found that quantities of nitrite of 0·71 mg. atoms N/m.^{3} and over were sufficient to affect the Winkler method. The interference occurs through the nitrite's liberating iodine from the potassium iodide and giving a greater quantity of iodine than would normally be released through the acidification of the manganic hydroxide precipitate in the presence of potassium iodide. The error is, of course, to overestimate the amount of oxygen present. 0·71 mg. atoms N/m.^{3} is quite a high figure for the sea, but as no nitrite estimations were made the extent of any error likely to arise was unknown. The modified Winkler method used to deal with hydrogen sulphide, however, also removes any interference due to nitrite.

Some of the sediments on the sea-bed in the region of Walvis Bay are populated by sulphate-reducing bacteria, whose activity results in the production of hydrogen sulphide. This gas, liberated into the overlying water, appears to coexist, in a dynamic state, with the dissolved oxygen (Durov and Turzhova, 1947). To obtain a true estimation of the oxygen content at a particular time and position it was necessary, therefore, to put an end to the oxidation-reduction reaction as soon as possible after sampling. Although Alsterberg's method (1926) would have been preferable we tried to accomplish this by using the Rideal–Stewart modification of Winkler's method, which could conveniently be carried out with the chemicals available on board. The method consists of a preliminary oxidation, carried out by treating the acidified water sample with potassium permanganate. When the reduction is complete any remaining permanganate is destroyed by the addition of potassium oxalate, after which the normal Winkler method is continued.

Parallel determinations on samples from Walvis Bay with both the Rideal–Stewart and unmodified Winkler methods gave the results shown in Table 1.

Table 1. *Dissolved oxygen content of water-samples from Walvis Bay*

	Dissolved O_2 content (c.c. O_2/l)	
Sample no.	*Unmodified Winkler*	*Rideal–Stewart Winkler*
1	0·00	0·03
2	0·00	0·09
3	0·00	0·11
4	0·05	0·13
5	0·30	0·38
6	0·46	0·51
7	0·64	0·80
8	0·68	0·88

Oxygen determinations on water-samples taken in Walvis Bay using both the Rideal–Stewart and unmodified Winkler methods. The samples have been arranged in order of concentration, and they were all analysed at the same intervals after collection.

A further test was carried out on four similar samples with the unmodified Winkler method. Two of the samples were analysed immediately after collection, while two were kept for 4 hr. before analysis. The first two showed respectively 0·41 and 0·39 cc. O_2/l. more than the second two. If this

reduction in the oxygen content of the second two samples was solely due to reduction by hydrogen sulphide, the result would indicate that a concentration of about 0·8 cc. H_2S/l. had been oxidized in the 4 hr. which elapsed. Unfortunately we had no opportunity of making more experiments of this nature, and it is not possible to say precisely how efficiently the Rideal–Stewart method accomplished the task which it was set.

TREATMENT OF THE PLANKTON SAMPLES

The microplankton catches (N 50 V samples) were worked up by a counting technique essentially similar to Hensen's method, as described by Steuer (1911). From the whole sample, thoroughly mixed by agitation in a spherical Stempel flask, subsamples were drawn off with an 0·5 ml. Stempel pipette and placed in a cell on a large slide, ruled with squares of approximately 1·8 mm. These can almost be contained within one field of the low-power objective ($\frac{2}{3}$ in.) of an ordinary compound microscope. The cell was originally intended for counting centrifuged samples at sea, where a cover-glass must be used. It measured approximately 10 × 24 of the squares and 0·4 mm. in depth so that almost exactly 0·3 ml. of fluid could be contained in it, trapped under a large rectangular cover-glass. For this work cover-glasses were not used during the early stages of the counts, but the cell was found very convenient to contain the larger volume of fluid while spreading it over the face of the slide with a mounted needle. When difficult rich subsamples prolonged the counting, or higher powered objectives than the $\frac{1}{6}$ in. were needed for identification, it was found that evaporation at room temperature allowed one to apply a cover-glass after some 45 min. Most of the counts took more than 2 hr. and continuous observation for a longer period increased personal error due to eye-strain, though a brief pause sufficed to counteract this. Thus the use of a cover-slip during the later stages, to prevent the preparation drying up, became an essential part of the technique.

The rulings on the face of the slide enabled one to resort to higher magnifications, or to recapitulate when necessary, without 'getting lost', and it was thus quite practicable to work through the whole subsample, using a large mechanical stage. A very abundant inshore pennate diatom, *Fragilaria karsteni*, has the habit of growing in very long ribbon-shaped colonies, and it was found that the numbers of frustules could be estimated rapidly, and with a high degree of accuracy, by measuring the ribbons under low power with a micrometer eyepiece, then measuring the width of a few individual frustules under high power and dividing appropriately.

For the method as a whole to be successful the subsample must not be so thick that individual cells or colonies obscure each other unduly. With large samples this was avoided by preliminary fractionization and adjustment of volume, using a large (5-ml.) Stempel pipette and measuring cylinders for added water. Errors were obviously increased by such a crude method, but could be reduced by making separate counts at different dilutions for the more difficult stations, and pooling the results; and by such expedients as counting large or conspicuous species at normal dilutions where the density of smaller dominant species necessitated further subsampling before they could be counted. When the general nature of the flora had become familiar it was nearly always found possible to judge the extent of fractionization and dilution needed from the settlement volume and macroscopic appearance of the sample. At worst two trials enabled the necessary adjustment to be made.

The main object of this line of work was to study the spatial distribution of the larger phytoplankton organisms in relation to the hydrological features of the area. Obviously such estimations can bear little direct relation to the total amount of phytoplankton present—it has long been known that there are many autotrophic organisms among the minute forms that escape the finest nets—but it is claimed that, so far as the diatoms and larger dinoflagellates are concerned, they show up the grosser quantitative differences quite fairly in areas such as this, where the gradient of population density is very

steep. The quantitative differences are so marked, as between the coastal current and the oceanic surface-water to the west, that even such crude measures as settlement volumes can be shown to be statistically significant.

The numerically estimated totals of Protophyta, and of dominant groups or species, when plotted logarithmically, showed distributional patterns in good agreement with hydrological features independently assessed. Moreover a 50% alteration, in either direction, of the values assigned to the contour lines made little difference to their position on the chart. Crude as the method undoubtedly is, errors of this magnitude are very unlikely and the counts are therefore believed quite fairly to represent the broad outlines of the distribution of such organisms as were retained by the finest grade of bolting-silk. All the counting was carried out ashore, while working at the Plymouth Laboratory.

The great variety of the Benguela current plankton is shown by the fact that although only diatoms and *Ceratia* were identified down to species, the raw counts include some 200 categories of organisms. This unfortunately makes it impracticable to publish them in full, but the tables of derived values, dealing with group totals and relative abundance of more important categories, show the number of categories observed during each estimation, in addition to volumes and fractions of samples examined. This should give some idea of the qualitative richness of the microplankton of the area in addition to its great quantity.

For the study of *relative* importance of the various categories these counts should be quite satisfactory since several hundred individuals were involved in most of them. More than 300 individuals were counted at 79% of the stations, and at more than half of these (42% of the total) over 600 individuals. Only at the very poor stations, where concentration (as opposed to dilution) might greatly have increased the manipulative errors, did the numbers fall below 300 per station. These poor samples constituted 21% of the total and the numbers of individuals counted in them ranged from 90 to 288 with an average of 209.

Changes in relative abundance are important when it can be shown that species or groups have 'indicator value'; that their distributions are mainly restricted to water-masses that can be distinguished by their physical attributes. When this can be established, plankton distributions may provide evidence of water-movement and of areas of mixing, of real value to the physical oceanographer and to fishery research.

It has proved impossible to complete group-sorting of the zooplankton collections in time to consider them fully in this report. The vertical net series for the first survey have been almost completely sorted, and individual zoologists able to work up some of the groups have come forward. In this general description of the plankton conditions, we have mentioned only such important (and often elementary) features as became apparent at the sorting stage, adding specific identifications confirmed or established by specialists whenever it has been possible to do so. Some reports on single groups have already appeared and acknowledgements to those who are aiding the work in this way will be found in the zooplankton section. Examination of second survey material has only been completed for pilchard eggs, larvae and post-larvae, the importance of which became apparent at an early stage. A preliminary account of their distribution has already appeared (Hart and Marshall, 1951).

Complete sorting of all groups, except Protozoa, Coelenterata, Copepoda and small nauplii (mainly of Copepoda), has been attempted. For the latter subsampling proved the only practicable procedure, and at a few very rich stations subsampling had to be adopted for some of the other groups also. Nearly all the work has to be carried out under a binocular dissecting microscope, since many of the animals were much smaller than their relatives in cold seas. We are very grateful to Dr M. V. Lebour, and others working at Plymouth who have occasionally corrected or confirmed provisional identifications for us.

ITINERARIES

Survey I (March)

On the afternoon of the 1 March 1950, the 'William Scoresby' proceeded southward from Lobito Bay towards the outer end of the first line of stations (WS 964, see Fig. 1). This course involved some two days steaming, and it was not until early on the morning of 3 March that the first indications of the Benguela current were met with. In 16° 13′ S., 11° 31′ E. the distance thermograph revealed a sudden decrease of sea temperature from 27° C. at 02.45 hr. to 20·5° C. at 03.45 hr. At the same time the echo-soundings showed a sudden increase in depth from 110 m. to 439 m. followed by a return to the shallower 110-m. level. During the day the temperature rose again, but not to its initial (tropical) level. Evidently the ship had crossed one of the most northerly patches of the cold upwelled water so characteristic of the Benguela system. This may possibly have been associated with the indentation of the continental shelf indicated by the soundings.

The projected position of the first station was reached just after noon on the 4th, and during the rest of that day six stations were completed, at intervals of some 18 sea-miles, as we worked eastwards in towards the land. The weather was moderately favourable at the first station (WS 964) and improved as land was approached. Station WS 970, marking the inshore end of the 'Möwe Point' line was completed at 01.27 hr. on the 5th, and the course was continued south-westwards working the five stations of the northern intermediate line (WS 971–5) throughout that day. The wind and sea increased as we proceeded offshore, but fortunately moderated again on the morning of the 6th when we reached the first full station position, WS 976 in 22° 50′ S. 11° 38′ E., the outermost station of the 'Walvis Bay Line'. This and the following day were spent in completing stations WS 976–9, and on the morning of the 8th, after stations WS 980 and 981, the ship went into Walvis Bay. Here some arrears of chemical analyses were dealt with and some useful information on local fishery matters was gleaned from some of the residents.

Leaving Walvis Bay on 9 March, the ship passed through large areas of discoloured water, mainly of an olivaceous colour, with small patches of a deeper brown or reddish colour. Surface samples were examined, showing immense numbers of diatoms with but few *Gymnodinium* spp. The more densely coloured patches contained a small dinoflagellate, which subsequent work on preserved material has shown to be *Peridinium triquetrum*. Seals (apparently fur-seals) were seen playing lazily in the discoloured water. Our course lay south-westwards, and the middle line of bathythermograph stations was completed by 04.38 hr. on the 10th. At 08.05 hr. the first full station of the 'Sylvia Hill' line was begun in fine weather, and the clear, almost metallic blue colour of the water here formed a sharp contrast to the turbidity of that inshore. The Nansen–Pettersson water-bottle was visible at a depth of 20 m. By the end of the station, however, the water was obviously more opaque, and steaming eastward we again passed through more discoloured patches within the hour, and continued to do so until 17.05 hr. At station WS 986 there was much macroplankton about the ship; many Ctenophores, mainly in a necrotic condition, and colonies of Salps, were taken out with the hand net. Small shoals of fish were seen, but could not be sampled.

The 'Sylvia Hill' line was completed before dawn on the 11th, and proceeding south-westwards again, on the southernmost line of bathythermograph stations, an otter trawl was used at WS 990. The catch contained several large hake, a fair selection of the other common ground-fish of the region, and some good specimens of Stomatopoda. The outer station of the 'Orange river' line, WS 996, was reached at 15.55 hr. on the 11th and the remaining stations of this line were continued in fine weather, being completed by 03.45 hr. on the morning of 14 March.

Further observations would, of course, have been desirable, but the commitments of the rest of the

programme, and the rather urgent need for repairs to some of the auxiliaries, was such that we had been fortunate in carrying out most of the coverage planned before proceeding to Simon's Town, where we arrived on 16 March.

Survey II (September–October)

The second survey of the current had not originally been contemplated, but preliminary examination of the results of the first survey indicated that a repetition would be very desirable, and subsequently a necessary alteration in the programme of the ship made it possible. It was decided that certain extensions to the programme would greatly enhance the value of the repeated stations. Details of this expanded programme were decided upon by Mr Clarke, and its value can readily be appreciated from the results obtained.

Leaving Simon's Town on 19 September 1950, we worked a series of bathythermograph stations (see Fig. 2) round the Cape of Good Hope, and up to the Orange river mouth where the ship arrived on 21 September. Numerous fur seals were encountered on this journey, and several fairly extensive patches of olivaceous coloured water were crossed. Full stations were worked in approximately the same positions as on the first survey, while the ship steamed out along the Orange river line, and this was completed on the 23rd. Our course now lay north-eastwards, repeating bathythermograph observations, and the inner end of the 'Sylvia Hill' line was reached on the 25th. The full stations WS 1064 and 1065 were completed by about midday on the 26th, and then a slight diversion was made to take some bottom samples to the north of the line. This included a circumnavigation of Hollam's Bird Island, a guano island concerning which the following extract is quoted from Dr Clarke's journal:

> By 1700 hrs. we had approached to within half a mile of Hollam's Bird Island. As we steamed over the shelf which surrounds the island, the echo-sounder showed several fish shoals, densely packed, in ten fathoms of water.
>
> The island is small and low, not rising more than forty or fifty feet in its highest part. . . . An elaborate sheerlegs is a conspicuous feature of the island, and its skeleton framework overhung the rock strandflat and adjacent breaking water, like some part of the wrecked architecture of an amusement park—even to the strings of electric lamps counterfeited by rows of cormorants sitting equally spaced along the struts of the sheers. Near this structure stood a small roughly built shed—the island is visited at times by the government guano collectors.
>
> The higher ground lay back from the landing place, and from these higher parts the cliffs fell away steeply, the yellowish rock face being boldly streaked with white spillings of guano. And everywhere, crowded thickly upon the slopes, and as far as the highest point, were the fur seals. As we came within half a mile we could hear their barking above the drumming of the surf. From a distance it was a dog-like noise, like many packs of hounds, only deeper in tone. The din must have been tremendous for anyone landing there and walking among the crowded seals. There were many hundreds of seals on this scrap of rock: I made no estimate, but Mr Currie put the population around 1300, probably more. The island with its multitudinous seals looked like a currant cake, of the kind children call 'flies' funeral'. The shiny coats caught the sun, and reflected so many black points, some in slow movement and some quite still, on the wet slopes and crags. Most movement was on the lower rocks, near the landing-place, where the heavy surf was lively with heads and flippers and the strandflat populous with seals coming and going from the water.
>
> Although I could only, from the distance at which we sailed, identify among the birds the cormorants on the sheers, there were obviously great numbers of birds grouped among the seals. At 1700 I counted flocks of about fifty cape gannets, fifteen cape cormorants and five southern black-backed gulls; and also five cape pigeons, although these were farther off.
>
> The visit to Hollam's Bird Island was worthwhile if only to have seen so much life on this tiny island off the barren 'Skeleton Coast'—life so teeming that only a scene in Antarctic seas is comparable. It brought home more vividly than anything else how real and astonishing are the effects of the productivity of the Benguela Current.

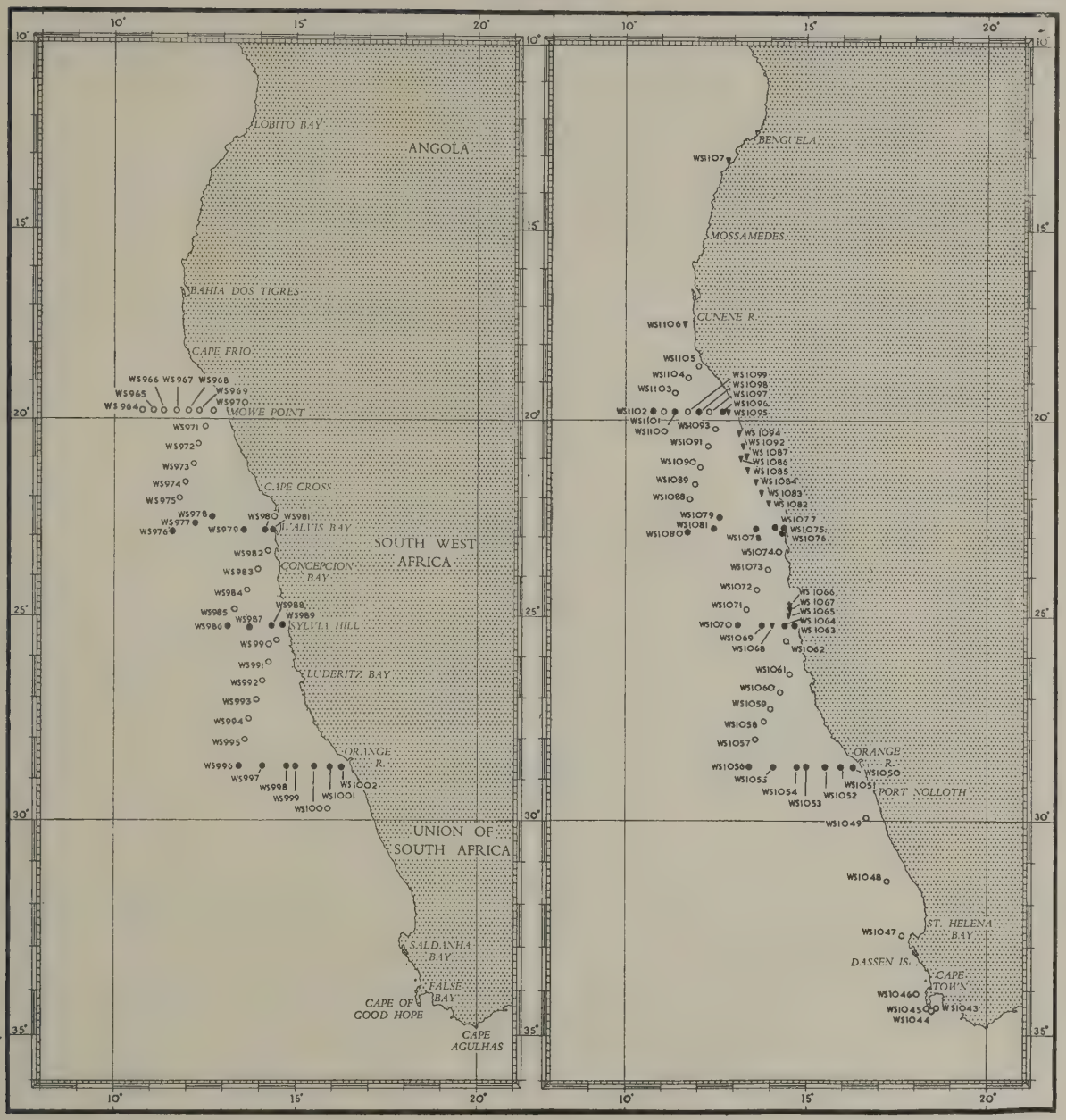

Fig. 1. Station chart, survey I, March 1950. Positions of 'bathythermograph and phytoplankton' stations are shown by open circles, those of 'full' stations by closed circles.

Fig. 2. Station chart, survey II, September–October 1950. Symbols as in Fig. 1. Solid inverted triangles indicate positions of bottom sampling-stations.

After visiting Hollam's Bird Island we completed the full stations of the central line, and the ship steamed towards Walvis Bay making bathythermograph observations at WS 1071–4. On the 29th the 'Walvis Bay' line was started and worked out to WS 1079, after which further station work was delayed by a strong southerly gale which set in. The ship was hove-to for two days while the gale increased to force nine (Beaufort), and not until the afternoon of 2 October did it abate sufficiently to permit us to continue observations, whereupon stations WS 1080 and 1081 were completed, and the ship sailed to Walvis Bay.

After we left Walvis on 6 October, a series of bottom-samples were taken up past Cape Cross (WS 1082–7), and then the bathythermograph observations were resumed, and continued up to Möwe Point, with two detours (WS 1092 and 1094) inshore for bottom sampling, *en route*.

In this area, and also on the 'Möwe Point' line station, numerous large shoals of fish were encountered. Here again, we quote from Dr Clarke's Journal:

9th October, 1950. In the early hours of today (0100 to 0430) the officer of the watch reported that the ship steamed through large shoals of small fish, like herring or pilchards. This was in position 20° 35′ S., 12° 55′ E. to 20° 10′ S. 12° 30′ E.

Again from 2015 to 2145 (around 19° 43′ S., 12° 36′ E.) we found ourselves passing multitudinous shoals of fish. It was a dark night, and I stood and watched the shoals scatter from our approaching forefoot, one after another, betrayed by a burst of greenish blue luminescence, so that the shape of each fish showed up in ghostly outline. Below the forefoot, and fanning out to port and starboard, the shoals were like the showery explosion of roman candles under water.

I counted a hundred shoals (each estimated at > 100 < 1000 fish) appearing in 4 minutes 23 seconds, or 0·4 shoal (> 40 < 400 fish) per second; the ship was then steaming at about eight knots.

The ship was stopped in an attempt to catch some of these fish with both baited hooks and jiggers, so that the species might be determined, but all efforts were unsuccessful.

Further station work was continued with two short interruptions to mark some whales, and the second survey completed on 12 October.

Two bottom-samples were taken to the north, at WS 1106 and 1107, to ascertain if the 'azoic' mud extended so far north. Approaching station WS 1107, between 14.15 and 15.21 hr. on 14 October, patches of blood-red water were observed, some 20–30 yards across, a bucketful was collected, and microscopic examination of preserved subsamples showed that the organisms causing the discoloration were almost certainly ciliate protozoa such as have previously been seen to cause red water elsewhere (see p. 255).

COASTAL GEOGRAPHY AND BOTTOM TOPOGRAPHY

The west coast of South Africa stretches in a more or less N.N.W. direction from the Cape to about 18° S., then continues north and N.N.E. into the Bay of Benguela. Practically the whole length of this coast is characterized by a narrow coastal belt of low-lying land gradually ascending to the high interior plateaux at a distance of about 80–100 miles inland. The coastal belt is fertile in the south, but gradually passes into scrub, and north of 30° S. is a truly arid desert. This desert, which continues to about 14° S., is known in South-west Africa as the Namib. It is almost completely waterless, although heavy dews occur, and the small annual rainfall (Fig. 3) generally occurs in a very short space of time, draining into the Atlantic almost as quickly. The dew is sufficient to support a very scanty xerophytic flora, but cultivation is only possible up country in the more fertile valleys. The presence of the desert is principally due to the cold water lying along the coast, which causes condensation from the lower layers of the air above it (Scherhag, 1937), and acts like a mountain range, leaving the land to leeward in its rain shadow. North of the desert, in Angola, the sand gradually gives way to wooded country within the range of the seasonal tropical rains.

Although in itself arid, the South-west African coast has a very large drainage area, extending across the interior to the western slopes of the Drakensberg mountains on the other side of the continent. Practically all of this drainage, however, is collected in the Orange river, and other rivers along the coast are only periodic torrents, during the summer rains in the south-west.

The topography of the sea-bed is shown in Fig. 4. It appears to be affected in a large degree by the

Orange river, for the great underwater promontory sweeping seawards from the river mouth suggests a considerable alluvial deposition from the great drainage system.

Although more data are still needed, the representation of such major features of the sea-bed seems adequate for our present purpose. The chart (Fig. 4) has been constructed from:

1. The most recent Admiralty Charts of the region.
2. Carte Bathymetrique Internationale. A IV (International Hydrographic Bureau, Monaco, 1938).
3. 'Meteor' expedition bathymetric charts (Stocks, 1941).
4. Soundings made by the 'William Scoresby'.

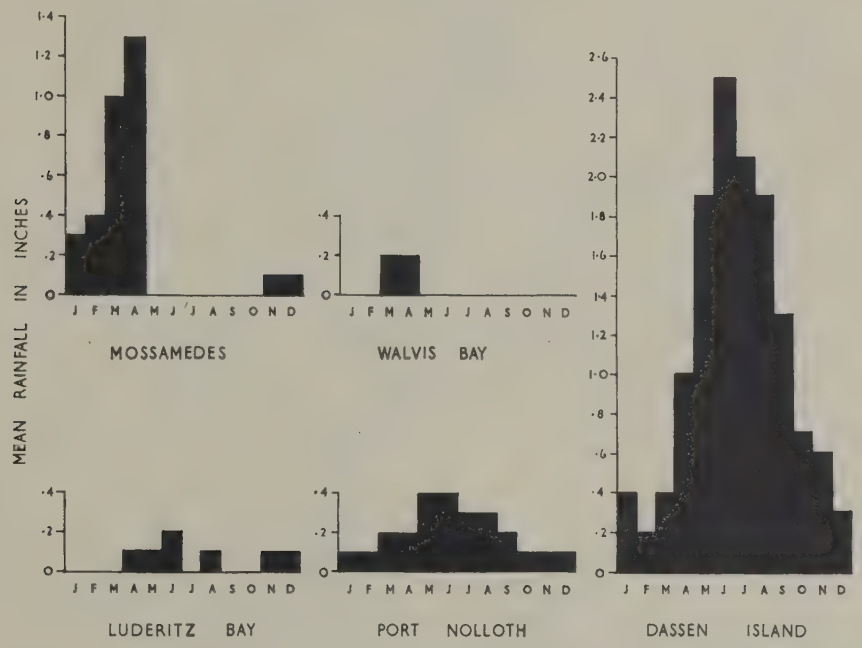

Fig. 3. Mean annual rainfall in inches, at five points on the South-west African coast: Mossamedes (15° 12′ S.), Walvis Bay (22° 56′ S.), Luderitz Bay (26° 39′ S.), Port Nolloth (29° 14′ S.), and Dassen Island (33° 26′ S.). (From data in Royal Naval Meteorological Service and South African Air Force, 1944.)

Over the greater part of the area covered by our surveys, the continental shelf, defined approximately by the 200 m. contour, is about 40 miles broad, widening to about 90 miles off the Orange river mouth, and to 70 miles off Walvis Bay. Off Concepcion Bay, in 24° S., there is a sharp indentation on the shelf edge, and as at Luderitz Bay the shelf is less than 20 miles broad.

North of 20° S. the shelf narrows, and between 16° and 13° S. is almost non-existent, the slope falling straightway from the coast into the depths of the Angola Basin. The shelf edge off Bahia dos Tigres is much dissected into deep valleys which extend to depths of 1000 m.

The bottom slopes away fairly steeply from the coast to the 100-m. contour along most of the coastline, and then more gradually to the shelf-edge, forming virtually a submarine plain, a feature most pronounced off the Orange river. From the shelf-edge there is a fairly gradual and constant slope to 3000 m., interrupted only off the Cape Peninsula where deep canyons are numerous between 500 and 3000 m., and in 20° S. where the continental slope is very gradual and at 1000 m. grows into a buttress forming the northern end of the Walvis Ridge.

The Walvis Ridge leaves this buttress in a westerly direction at 3000 m., and runs southwards and then to the west again to link up with the central Atlantic Ridge. In 25° S., 6° E. there is a prominent

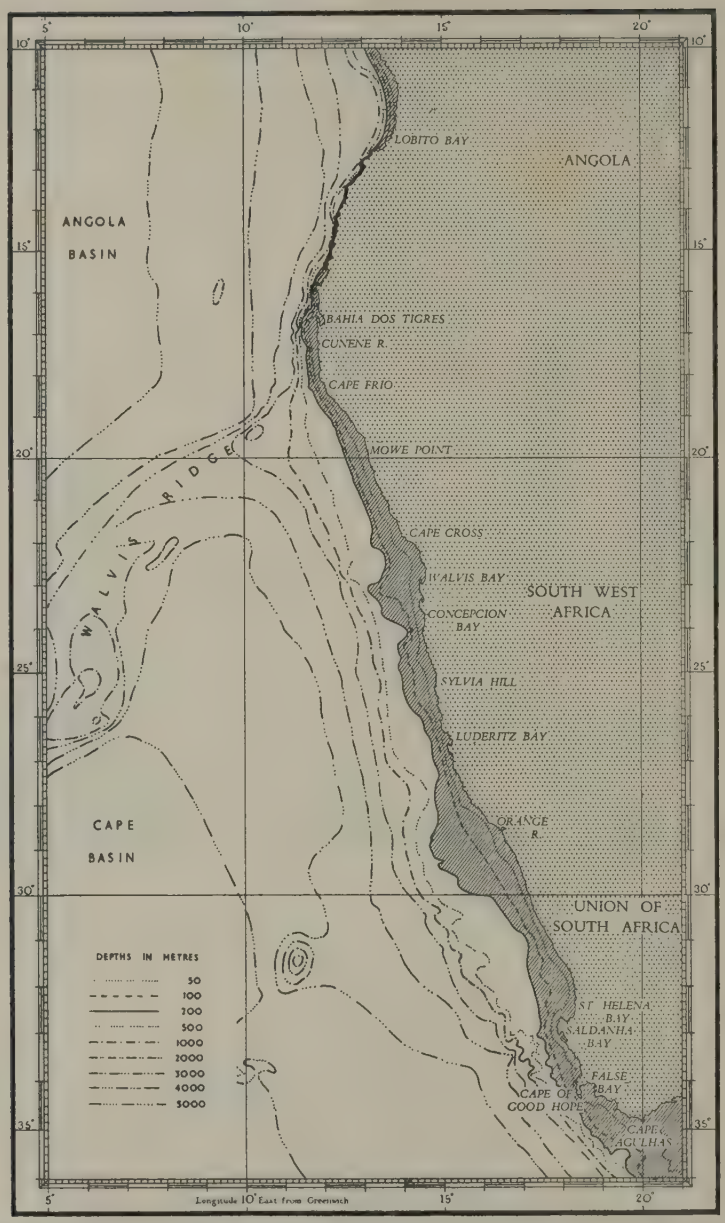

Fig. 4. Topography of the sea-floor of the South-west African region. Depths in metres. The hatched area shows the extent of the continental shelf. For origin of data see text.

peak on the ridge rising to less than 1000 m. from the surface. Soundings over this deeper part of the ridge are scarce and there may be a gap in about 22° S., but even so it can be little more than a break in the 3000-m. contour, and the results of the 'Meteor' expedition have already demonstrated the significance of this ridge in the circulation of the deeper waters. The Walvis Ridge forms a very effective barrier to northward movement of the Antarctic bottom water, the potential temperature of the bottom water in the Cape Basin being less than 1·0° C., while in the Angola Basin it averages more than 2·0° C. (Wust, 1935).

In 31° 20′ S., 11° 20′ E., there is what appears to be a sea-mount rising from 4000 m. to within 1000 m. of the surface, but this is evidently an isolated feature.

Soundings taken on the 'William Scoresby's' line of stations are plotted in the respective vertical sections (Figs. 12–18, 22, 23, 25–30). In these diagrams the vertical scale is, of course, very exaggerated (about 320 times). The absence of much shelf, with development of a fairly gradual slope, is clear on the most northerly section, while on the Walvis line there are two shelves about 25 miles broad, the upper just over 100 m. deep, and the lower at 300 m. At Sylvia Hill the coast slopes away steeply to a narrow shelf at 200 m., while on the Orange river line the shelf is much broader, about 50 miles, at 175 m. This latter represents the northerly part of the promontory referred to off the Orange river.

METEOROLOGY

Wind systems

The movements of the sea are so closely linked with those of the overlying atmosphere that any account of the oceanographical phenomena of a region must necessarily take into consideration the prevailing meteorological conditions. Fortunately, off South-west Africa these seem to fluctuate so regularly (apart from minor variations) that a normal or 'average' pattern can be formulated, which serves as a background against which the data relating to the periods of these two surveys can be considered. The general account which follows is based upon data collected by the Meteorological Services of the Royal Navy and the South African Air Force (1944), supplemented by the work of Dr S. P. Jackson (1951) who has long been interested in the weather of South-west Africa.

The wind system over the South-west African waters depends mainly upon the subtropical high-pressure region which overlies the South Atlantic. The latitudinal axis of this anticyclonic centre is situated between 26° and 30° S. From the centre the pressure gradient decreases gradually to the north, but to the south, where it borders on the zone of the 'westerlies', the gradient is much steeper. Round this high-pressure region the winds blow anti-cyclonically, so that off South-west Africa, which lies in the eastern side of the pressure system, the winds are predominantly south or south easterly. The coastal region, however, lies in the transition belt between the oceanic and continental pressure systems, and so in the proximity of the coast the winds become modified by the fluctuations between the two systems. It is necessary, therefore, to distinguish two separate wind regions—that offshore where the South Atlantic anti-cyclone acts alone, and the other inshore, where both the oceanic and continental pressure systems play a part.

The trade wind

In the summer, when the anti-cyclone lies in about 30° S., strong constant winds are produced, which affect the whole oceanic region northwards from the Cape. About 80–85% of these winds are south-easterly, and they blow with an average velocity of 11–21 knots. At the Cape peninsula these 'south-easters' are a prominent feature of the summer climate, but the strongest winds are farther north, between 25° and 30° S. North of 25° S. both the velocity and constancy of the trade winds diminish.

In winter time the anticyclone moves northwards and intensifies slightly—generally about 2 millibars higher than in summer—so that the centre of highest pressure comes to lie in approximately the latitude of Luderitz Bay (26° S.). Owing to the steep southward pressure gradient the trade winds in 30° S. then become intermittent. This northward displacement of the pressure system brings the Cape region under the influence of the depressions of the westerlies, which, travelling eastwards from the south-west Atlantic, bring rain to South Africa, accompanied by the attendant cyclonic variation of the winds. The effect of these depressions extends as far north as Port Nolloth, where they produce

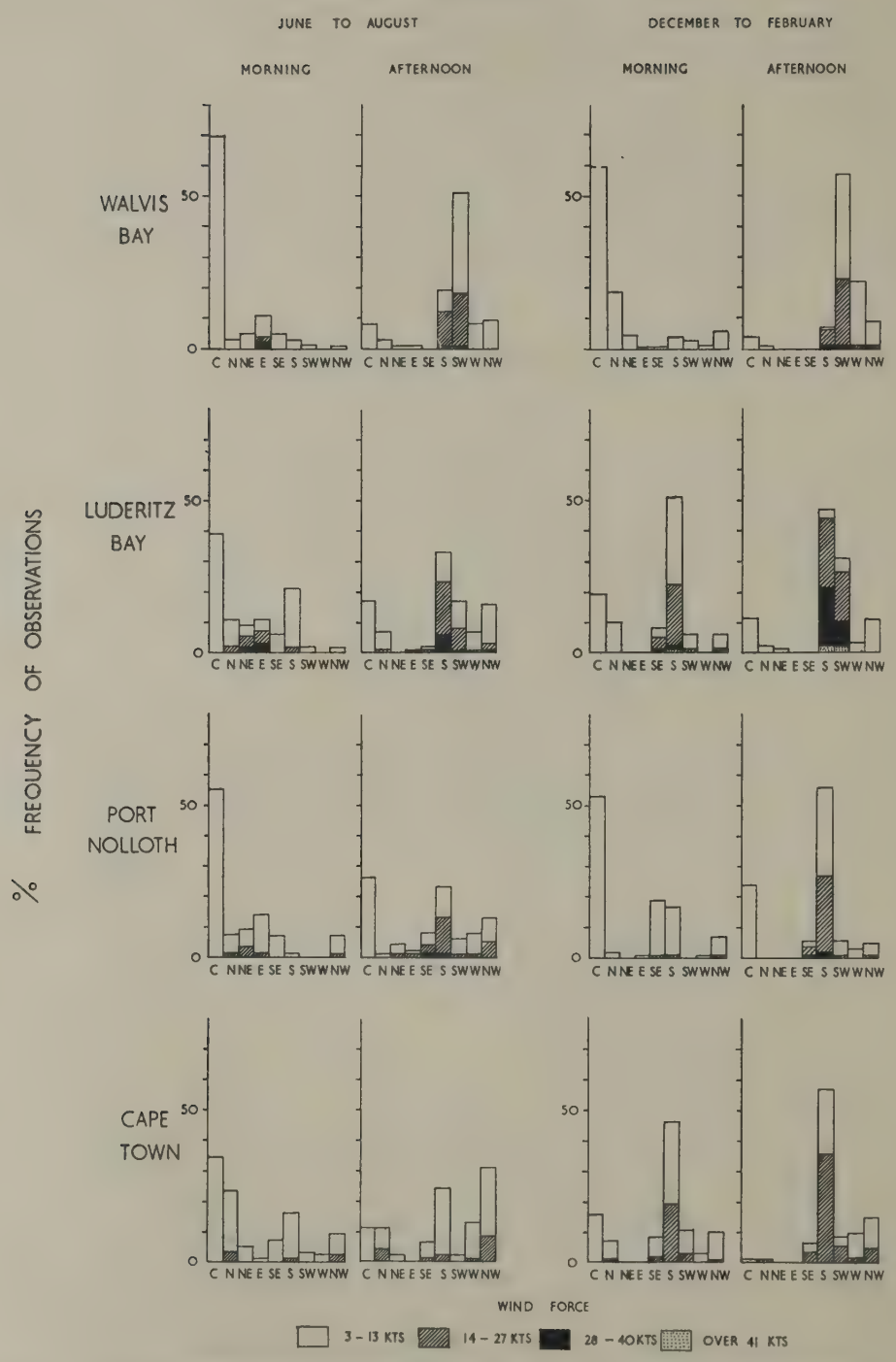

Fig. 5. Percentage frequency of coastal winds in winter and summer. (From data in Royal Naval Meteorological Service, etc., 1944.)

a light, but quite pronounced winter rainfall (Fig. 3) which does not occur in the more northerly parts of South-west Africa. The region of strongest winds also shifts north in winter, and lies in about the latitude of Walvis Bay, where 30% of the trade winds have a velocity of over 16 knots.

The coastal winds (Fig. 5)

Although the inshore region remains under the influence of the South Atlantic anti-cyclone, the winds are also affected by the variations in pressure over the continent, and as this fluctuates diurnally with the heating and cooling of the land, so the coastal winds develop a marked diurnal variation (Fig. 5). During the day, when the land is warmed up, the overlying air mass becomes light, and this causes the cooler, more dense air over the sea to flow inland. This continues until equilibrium is regained, and stable conditions are once more set up. On the whole these coastal winds, while they last, are stronger than those at sea, but when the trade is blowing strongly over the open ocean one generally finds the coastal winds are also stronger.

In summer (December–February), when the anti-cyclone is in its southern position, south winds are prevalent on the coast as far north as Luderitz Bay (Fig. 5), generally having an easterly component in the morning. This seems to be the effect of the anti-cyclone exerting its influence on the relatively stable air mass over the coastal waters and land during the night and early morning. As the land warms during the day, however, the wind veers round to the south and south-west and intensifies, reaching at Luderitz an average velocity of 22–27 knots. This may occur fairly early in the day, and the sea-breeze then continues until after nightfall when the pressure systems become balanced, and the anti-cyclone once again becomes the dominating influence. It will be remembered, however, that in summer the anti-cyclone has its greatest effect in the Luderitz Bay region, and that north of this its influence steadily decreases, so that at Walvis Bay the stable air mass during the dark hours appears to be little affected by the anti-cyclone, and the conditions experienced there during the night are either complete calms or light northerly winds. As the day progresses, and the temperature effect comes into play, the wind *backs* to the west and then S.S.W. from which the sea-breeze develops just after noon, and blows with a mean force of 11–16 knots.

In winter, as might be expected with the northward shift of the pressure systems, the seasonal variation is much more pronounced south of Orange river than on the more northerly part of the coast. With the westerly depressions, the Cape receives winds more or less evenly distributed between north and south from the westerly sector. A marked feature of the winters is the north-westerly gales, which along with south-westerly weather are associated with the passage of the depressions. These features are less prominent at Port Nolloth where the trade and the diurnal variations begin to take effect.

Occasionally, when the anti-cyclone is not strongly developed near the coast, small depressions form close to the shore, and move northwards. On these occasions the sky remains cloudy, and a light north-west wind sets in with a force of about 7–10 knots. These conditions have a remarkable effect upon the sea temperature, which increases suddenly and has been known to reach as much as 23·9° C. at Walvis Bay.

At both Luderitz Bay and Walvis Bay there is a marked increase in easterly winds during the mornings in winter time (Fig. 5), but in both cases they are replaced with the much stronger south-westerly breeze in the afternoons. Pressure is high on the continental plateau in winter and, coupled with the lower pressure over the coast, leads to an outward push of air from the plateau. This usually becomes obliterated later in the day, partly by a diurnal variation of the east wind itself further inland. Amidst these easterly winds, when conditions are favourable, the noteworthy 'Berg winds' occur, which, blowing with considerable force towards the coast, make conditions extremely unpleasant on account of their high temperature compared with the generally cool coastal climate.

The Berg winds are extremely hot, dry winds which blow seawards across the desert, carrying much sand and dust. They may last from a few hours to several days. A temperature of 115° F. was recorded at Port Nolloth one day during a Berg wind. The highest recorded at Walvis is 104° F. but the average lies about 90° F. These winds are most frequent in winter, but can occur whenever the pressure gradient and heating of the surface air inland is suitable. When the 'Willlam Scoresby' visited Walvis Bay on 5 October 1950, a typical Berg wind was encountered. It blew for 4 or 5 hr. at 17–21 knots and produced a fine deposit of sand all over the ship. The air temperature reached 99° F. and the wind was uncomfortably dry. The Berg wind does not have much effect over the sea, for coming up against the cool dense air over the water the light hot air diverges upward, away from the sea surface.

In the coastal region, then, the principal wind of force is the sea-breeze, or 'soo-oop-wa' (as the natives call it), S.S.W. in the north and more southerly in the south. Jackson (personal communication) reckons that the sea-breeze probably has a fetch of some 80–100 miles over the sea, that is from its divergence from the south-east trade.

Weather preceding and during the surveys

There are not very many settlements along the desert coast of South-west Africa, and consequently the number of stations which make regular climatological observations is very small. Fortunately, however, records are maintained at Walvis Bay, Luderitz Bay, and Alexander Bay and these are used by the South African Weather Bureau in the construction of synoptic charts of the South Atlantic and South African region. Although we have not had access to the original data we have seen the synoptic charts published at Pretoria and have extracted the data for these three coastal stations as accurately as possible.

While shore observations are useful up to a point, observations at sea would have been much more desirable, but the sparsity of observing ships in the region during the survey makes it impossible to construct a complete enough picture. Most of the observations at sea are made on the main shipping route from Capetown to Sierra Leone, well outside the area of our survey. Such observations as there are, however, have been listed in Table 2, and do serve to show the constancy of the offshore winds, nearly all the observations, at least during survey II, lying in the south to east quadrant.

The only estimate, therefore, of the weather conditions preceding the surveys must be based on the observations made at the three coastal stations; and although the importance of the diurnal variations of the inshore winds has already been explained, all the synoptic charts are based on observations made once daily, at 08.00 S.A.S.T. These shortcomings of the records at our disposal have to be accepted, but must be borne in mind in interpreting the data.

The observations from the three shore stations for the periods preceding and during the surveys are given in Table 3. It can be seen that before survey I the weather at Walvis Bay had been calm or northerly, while at Luderitz Bay, right up to the time the ship visited the locality, the winds had mainly been southerly. At Orange river there had been very little wind for the whole month preceding and during the Survey.

Prior to Survey II, however, conditions were very different. Both Walvis Bay and Luderitz Bay had experienced much stronger winds, mainly from between south and west. As on the first survey, Orange river experienced comparatively calm weather.

So much for conditions on the coast. The constancy of the trade wind has already been shown from the observations at sea (Table 2). From the synoptic charts we can get some further information upon the state of these winds. It has not been considered advisable to calculate the vectors and velocities of the oceanic winds from the isobars, as they are based on so few recording stations. Regular observations come from the South African coastal stations, Tristan da Cunha and St Helena, and the observa-

tions of any ships in the neighbourhood are also included. But considering the vastness of the area affected, these few points must only allow a very approximate picture to be drawn.

The anti-cyclone rarely appears as a single entity, but is usually composed of several distinct high pressure centres slowly travelling across the Atlantic in an easterly direction towards South Africa. When one of these has passed, conditions become more diffuse until the next high pressure centre takes control. The cycle appears to average about four days, but it should be noted that the wind is dependent on the pressure gradient between the anti-cyclone and the lower pressure regions to north and east, and consequently does not vary directly with the position of the anti-cyclone.

Table 2. *Ships' observations (positions approx.) of the wind at sea during the 'William Scoresby' surveys**

Date 1950	*Latitude*	*Longitude*	*Wind (vel. in knots)*
5 March	24° 20′ S.	8° 20′ E.	S.S.E. 18
8 Sept.	29° 40′ S.	11° E.	S.E. 12
13 Sept.	15° 00′ S.	8° E.	S.E. 18
13 Sept.	19° 20′ S.	5° E.	S.E. 24
13 Sept.	25° 40′ S.	9° E.	E.S.E. 24
14 Sept.	26° 30′ S.	7° 40′ E.	S.S.E. 18
15 Sept.	20° 20′ S.	10° 30′ E.	S.E. 12
15 Sept.	22° 20′ S.	8° 40′ E.	S.S.E. 18
16 Sept.	27° 00′ S.	12° 10′ E.	S.S.W. 6
17 Sept.	27° 00′ S.	14° 00′ E.	S.E. 12
17 Sept.	22° 20′ S.	8° 10′ E.	E.S.E. 24
17 Sept.	29° 30′ S.	11° 00′ E.	S. by W. 6
17 Sept.	25° 30′ S.	5° 00′ E.	S.E. 18
19 Sept.	25° 50′ S.	10° 30′ E.	S. by E. 24
20 Sept.	27° 40′ S.	12° 00′ E.	S.S.E. 18
20 Sept.	22° 00′ S.	9° 00′ E.	S.S.E. 24
24 Sept.	21° 40′ S.	8° 20′ E.	S.E. 6
25 Sept.	19° 40′ S.	6° 00′ E.	S.S.E. 12
25 Sept.	27° 40′ S.	9° 00′ E.	N.W. 6
26 Sept.	29° 20′ S.	12° 40′ E.	W. 12
27 Sept.	20° 00′ S.	10° 40′ E.	S.S.E. 12
28 Sept.	29° 20′ S.	13° 40′ E.	W. 18
28 Sept.	15° 40′ S.	8° 30′ E.	S.E. 12
28 Sept.	23° 10′ S.	7° 00′ E.	S. 12
30 Sept.	29° 30′ S.	14° 20′ E.	S.S.W. 18
30 Sept.	26° 00′ S.	11° 30′ E.	S.S.E. 12
30 Sept.	16° 50′ S.	5° 10′ E.	E.S.E. 30
1 Oct.	21° 10′ S.	7° 30′ E.	S.E. 30
8 Oct.	18° 30′ S.	11° 20′ E.	N.N.W. 6
8 Oct.	19° 20′ S.	5° 30′ E.	S.S.W. 6
10 Oct.	15° 20′ S.	7° 10′ E.	Calm

* Compiled from information collected by voluntary observing ships for the Meteorological Office.

In February and March 1950, the pressure gradient was not so pronounced as in September–October, and the centres of high pressure lay rather farther south in February and March, in about 30° S. Moreover the anti-cyclone in the September–October period was more intense, and frequently associated with quite marked low-pressure areas over the coastal region. The trade winds were, therefore, stronger and more constant before and during survey II.

Regular observations of wind were of course maintained aboard the 'William Scoresby' throughout both surveys, and these have been rather useful in illustrating some of the short-term effects on the water movement.

During survey I, after the ship left Lobito, the wind was fairly light from the south-westerly sector,

but steadily increased in force and backed to S.S.E. as the outer end of the Möwe Point line was reached. The wind here was blowing with a force of 4–5 Beaufort, but became lighter and veered to the south as land was approached. As we proceeded offshore to the seaward end of the Walvis Bay line it once more became S.S.E. but rather more variable in force, and when Walvis Bay was reached

Table 3. *Coastal winds*

Day	*Walvis Bay*	*Luderitz Bay*	*Alexander Bay*	*Walvis Bay*	*Luderitz Bay*	*Alexander Bay*
		February			*September*	
1	Calm	S.S.W. 30	—	S.W. 6	N.W. 6	S. 6
2	Calm	S. 30	Calm	S.W. 6	Calm	—
3	Calm	S. 30	—	S.S.W. 12	—	—
4	N. 6	S. 12	Calm	S.W. 18	—	W. 6
5	Calm	Calm	—	S.S.W. 18	—	S. 6
6	N.W. 6	S. 18	—	S.W. 18	S.W. 18	Calm
7	Calm	N. 6	S.E. 12	S.W. 18	S.W. 24	Calm
8	Calm	N. 6	Calm	S.W. 6	S.W. 18	S. 6
9	S.S.W. 6	S.S.W. 12	—	W.N.W. 6	Calm	—
10	N. 6	S.W. 18	S.S.E. 6	S.S.W. 6	N.W. 12	—
11	Calm	S. 18	—	S.W. 12	Calm	Calm
12	Calm	S. 12	S.E. 6	S.S.W. 12	S.S.W. 12	Calm
13	Calm	S.S.E. 12	Calm	W.S.W. 12	S. 36	S.E. 6
14	Calm	S. 6	Calm	N.N.W. 12	S.S.W. 24	S. 6
15	N. 6	S. 18	Calm	Calm	N. 6	N. 12
16	Calm	S. 6	Calm	S.W. 18	Calm	—
17	Calm	Calm	—	—	—	—
18	Calm	Calm	Calm	Calm	Calm	S. 6
19	Calm	S.S.W. 18	—	S. 12	—	S. 6
20	—	—	S. 6	W.S.W. 30	S.W. 30	—
21	N. 6	S.E. 6	Calm	S.W. 6	S.W. 30	—
22	N.W. 6	—	Calm	W. 6	S.W. 24	S. 6
23	W.N.W. 6	—	Calm	S.W. 6	W. 6	—
24	Calm	—	Calm	N.N.W. 6	S. 6	—
25	Calm	—	Calm	W.S.W. 6	W.S.W. 6	S. 6
26	Calm	—	—	S.S.W. 24	S.W. 18	Calm
27	S.S.W. 6	Calm	Calm	S. 18	S.S.W. 30	Calm
28	Calm	S. 6	Calm	S.S.W. 12	W.S.W. 18	Calm
29	—	—	—	S.W. 6	N.N.E. 6	Calm
30	—	—	—	S.W. 30	S.S.W. 24	—
		March			*October*	
1	S.W. 6	S.S.W. 12	Calm	S.S.W. 12	S.S.W. 30	—
2	N. 6	S.S.W. 30	S.S.E. 6	W.S.W. 6	S.W. 12	Calm
3	N.W. 6	—	S.S.E. 6	Calm	Calm	Calm
4	Calm	S. 6	—	S.S.E. 12	S.W. 6	Calm
5	S.W. 6	S. 6	—	E.N.E. 6	S.W. 12	Calm
6	Calm	S. 18	Calm	W.S.W. 6	Calm	Calm
7	Calm	S. 6	Calm	W.S.W. 6	Calm	—
8	Calm	S.W. 12	Calm	—	S.W. 30	—
9	N.W. 6	—	Calm	S.S.W. 6	N. 6	S. 6
10	Calm	Calm	Calm	—	—	W. 6
11	—	—	—	S.W. 12	Calm	Calm
12	—	—	—	S.W. 18	Calm	Calm
13	Calm	S.S.W. 6	—	S.S.W. 6	S.W. 12	Calm
14	Calm	—	Calm	S.S.W. 12	S.W. 24	—

Wind direction and velocity in knots, extracted for the three stations Walvis Bay, Luderitz Bay and Alexander Bay, from the synoptic charts of the Daily Weather Bulletin, 08.00 S.A.S.T. issued for the above months of 1950 by the Weather Bureau, Pretoria.

it died away completely. These calm conditions persisted until the inner end of the Luderitz line, but towards the Orange river line the wind built up again. It did not, however, become very strong—force 3–4 from the east of south. Off the Orange river mouth the wind dropped.

On Survey II the wind was light after we left Simon's Town, but increased after Saldanha Bay to force 4–5 and remained so until the seaward end of the Orange river line, except for a short calm spell off the Orange river mouth. The passage north to Hollam's Bird Island was very calm, but as we steamed seawards the wind increased from west of south, remaining between S.S.W. and S.S.E., force 4–5, up to Walvis Bay. The course seawards from Walvis Bay was attended by an increasing southerly wind which reached gale force at the outer end of the line, and the ship was hove to against this for nearly two days. The wind then fell quickly and the ship returned to Walvis Bay in light northerly airs. At Walvis Bay the Berg wind already mentioned was encountered, and conditions remained variable with a fair proportion of north-westerly wind up to Cape Frio, north of which the passage became increasingly calm.

SURFACE-CURRENTS

Previous data

Since the ship was working to a strict time-schedule it was impracticable to make any direct observations on the amount of set and drift to which she was subjected. A few occasions, however, presented themselves when trustworthy fixes (stellar or shore) could be correlated with an uninterrupted passage of the ship, thereby giving an estimate of the amount of drift due to wind and currents. With accurate wind observations it was then possible to get a fairly good idea of how much of the drift was caused by the currents alone. These data, although useful in relation to the other oceanographical observations, are insufficient to give any comprehensive picture of the circulation, and for this it has been necessary to draw on other sources of information.

In the South Atlantic Ocean the surface-currents take the form of a large anti-cyclonic gyral of water movement, a circulation impelled principally by the south-east trade winds. These drive the surface water in a westerly direction away from the African coast, and reaching South America it is returned southwards in the Brazil current, and eventually back to Africa in a current flowing more or less in the same direction as the Southern Ocean current but separated from the latter by the subtropical convergence.

Off the South-west African coast there is, therefore, a wind-driven transport of water, principally to the west but rather more northerly in the south of the region (Table 4). It has already been noted that the south-east trade, although very constant in force and direction offshore, becomes much more variable nearer the coast in the proximity of the continental shelf, and consequently, considering purely a wind-driven circulation, one would expect the currents also to behave with much greater irregularity in this region. Unfortunately very few current observations have been made in the coastal region since it lies off the track of the main shipping lanes, but sufficient exist to confirm the irregular

Table 4. *Mean set and drift of the south-east trade wind drift*

	Latitude 12°–18° S.		*Latitude 18°–24° S.*		*Latitude 24°–30° S.*	
	Mean set and drift	*No. of obs.*	*Mean set and drift*	*No. of obs.*	*Mean set and drift*	*No. of obs.*
Nov.–Jan.	244° 2 miles	141	273° 4 miles	146	316° 5 miles	175
Feb.–April	248° 3 miles	153	280° 4 miles	157	304° 4 miles	165
May–July	285° 3 miles	164	312° 3 miles	170	333° 3 miles	180
Aug.–Oct.	280° 4 miles	160	297° 4 miles	181	314° 4 miles	189

After Hydrographic Department, 1939.

nature of the sets (Mühry, 1864; Koch, 1888; Hessner, 1892; Walther, 1893; Reincke, 1896; Bachem, 1896; Gilchrist, 1903; E.K., S.M.S. 'Sperber', 1907; Pohlenz, 1908; Müffling, 1911; Clowes, 1954), and the British Admiralty Pilot (Hydrographic Dept., 1939), p. 48, remarks with regard to the coastal waters: 'The general set of the current southward of the Congo river is parallel with the coast in a northerly direction at the rate of from 10 to 25 miles a day; but it is very irregular, both in direction

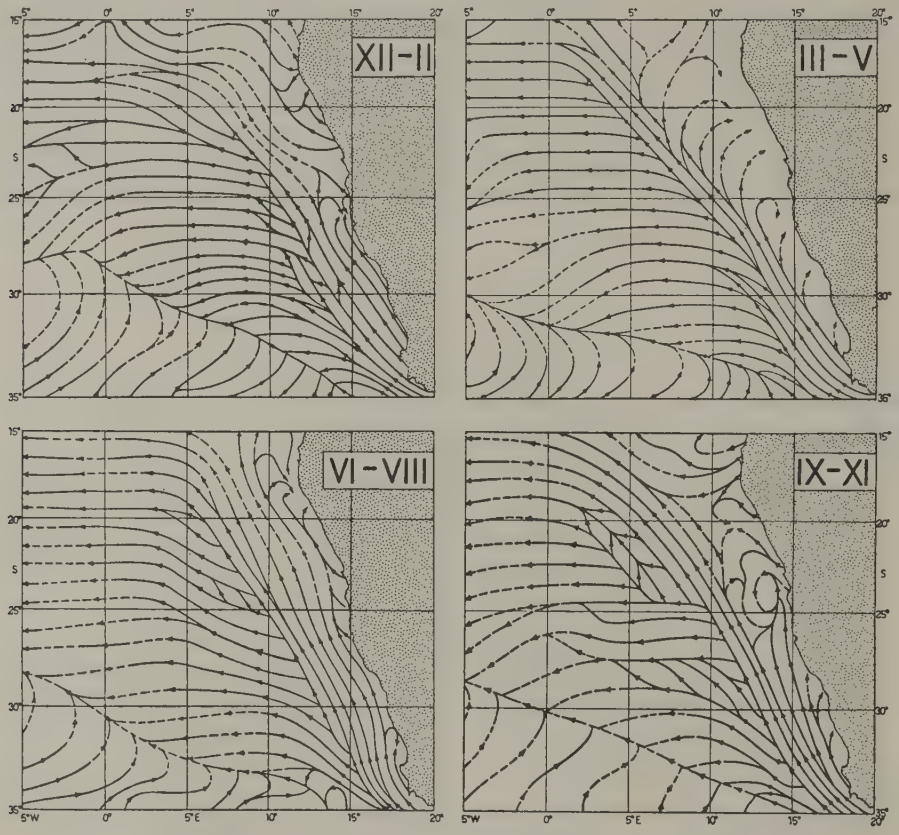

Fig. 6. Charts of surface currents for the four quarters of the year. After Defant, 1936.

and velocity, for sometimes, between October and June, but principally in March, April, and May, the direction of the current is completely reversed, and is found setting southward, and sometimes south-eastward.'

Defant (1936) has analysed the Dutch current observations, and meaned them for four quarters into one degree areas (1° longitude by 1° latitude), and concludes from his analysis (Fig. 6):

Ein Blick auf diese Stromfelder lehrt, dass das Charakteristische in ihnen die in allen Monaten wieder mit nicht zu überbietender Deutlichkeit auftretende *einseitige Divergenzlinie* ist; sie läuft nordnordwestwärts längs der Küste Südwestafrikas von etwa 30° bis über 20° südl. Br.; im Süden ist ihr Abstand von der Küste rund 160 sm, im Norden 300–350 sm. Das Gebiet ostwärts dieser Divergenzlinie, das ist gleichzeitig das Gebiet des Kontinentalabfalles und des Schelfes, hat eine Strömung nordnordwestwärts, also *parallel* der Diskontinuitätslinie und mehr oder minder auch parallel dem allgemeinen Küstenverlauf. Das Gebiet westwärts der Divergenzlinie hat im wesentlichen einen Strom nach Westen.

This interpretation of Defant's appears to correspond fairly well with the data in the possession of the Meteorological Office, the position of Defant's N.N.W. current being similar to that pictured by

the Meteorological Office current charts and more or less on the main shipping lane from Capetown to Sierra Leone.

The current-system of the region affected by the south-east trade wind seems clearly explicable on these lines, but although such an average picture may suffice for navigational purposes even in the more variable inshore region, it cannot assist in the interpretation of the hydrological conditions observed there. The irregularities already referred to show how much the inshore currents must depend upon local wind and local conditions generally. For a significant interpretation of the water movements here a synoptic rather than an 'average' picture would be needed. Existing data do not suffice for this, but a practicable working compromise has been attempted by correlation of the 'William Scoresby's' meteorological observations with the oceanographic data, and with the meteorological records of such other ships as were in the vicinity at the same time.

Currents during the surveys

In March 1950, on the passage southwards from Lobito Bay, the first appreciable effect of current was felt south of Bahia dos Tigres, where a moderate set to the north-east was noted. On the most northerly line of stations (WS 964–70) an allowance of 1° was made on the shoreward course for northerly set, and this maintained a latitudinal line of stations, but it is impossible to say just how much of this was the effect of current as distinct from the wind. At the stations on the outer end of the Walvis Bay line, however, a northerly set of about 1 knot was encountered with a light wind; the observed position of station WS 978 lying 16 miles north-north-east of its intended position. This northerly set was found at the offshore end of the three lines of full stations, and on the Walvis Bay and Sylvia Hill lines gradually became more easterly as land was approached, until at the inshore end of these lines the set was E.N.E. with negligible wind effect.

At the inshore end of the most southerly line, just off the mouth of the Orange river, the set appeared to be S.S.W., against a light wind from the same quadrant.

On the second survey, in spite of the stronger winds, little genuine current effect was recorded. Inshore at Orange river mouth, the ship, while lying-to for the night, showed negligible movement in completely calm conditions. Seawards, however, between WS 1052 and 1053 there was a northwards drift of 14 miles in 14 hr., but this may have been due to the wind. Between WS 1057 and 1061, the first pure current-effect was noted, the ship being set 065° at ½ knot with no wind, and at WS 1063 a slight north to north-east drift was probably due to the light south-west wind, and current must have been almost absent. These conditions continued between WS 1064 and 1067 and on the circumnavigation of Hollam's Bird Island there was no current at all. From 24° 02′ S., 13° 51′ E. to 22° 46′ S., 14° 20′ E. the current set 035° 10 miles in 12½ hr., and later a similar set was observed off Swakopmund where the vessel was stopped and drifted 035° for 3–5 miles in 5 hr. (0·7 knot). Again when stopped off Pelican Point lighthouse at WS 1076 the set was 035° 0·7 knot with no wind. The tide was on the flood then at Walvis Bay, and this may have accounted for the set.

From WS 1081 to Walvis Bay no drift was experienced, and a perfect course was made. As the winds were very light it is probable that there was negligible water-movement. After departing from Walvis Bay no drift of any consequence was encountered, and currents were disregarded in setting courses.

Summing up, the set on both surveys appears to have been very little, but when it was observed it was generally in a northerly direction in the offshore region, becoming more easterly nearer the land. The S.S.W. set off the Orange river is inexplicable at the moment, and it is impossible to say how much tidal streams were responsible for the E.N.E. sets experienced inshore.

OBSERVED DISTRIBUTION OF TEMPERATURE AND SALINITY

This section will be devoted to a description of the horizontal and vertical distribution of the physical and chemical properties of the waters which were surveyed. In the following sections an attempt will be made to relate these observed distributions to the prevailing meteorological conditions and the geography of the area with a view to elucidating the mechanism underlying the process of the upwelling and its fluctuations as we found them.

(*a*) (*b*)

Fig. 7 (*a*). Distribution of sea surface-temperature (° C.), survey I, March 1950. (*b*) Distribution of sea surface-temperature (° C.), survey II, September–October 1950. Both compiled from station observations and distant-reading thermograph records.

As the water masses under consideration exhibit a general northward trend, it will be more convenient to treat the results of both surveys from south to north, and not, therefore, in the chronological order of the stations worked during survey I.

The charts showing the distribution of surface-temperature (Fig. 7) and surface-salinity (Fig. 8) show that on both surveys the isotherms and isohalines ran more or less parallel to the coast. Within

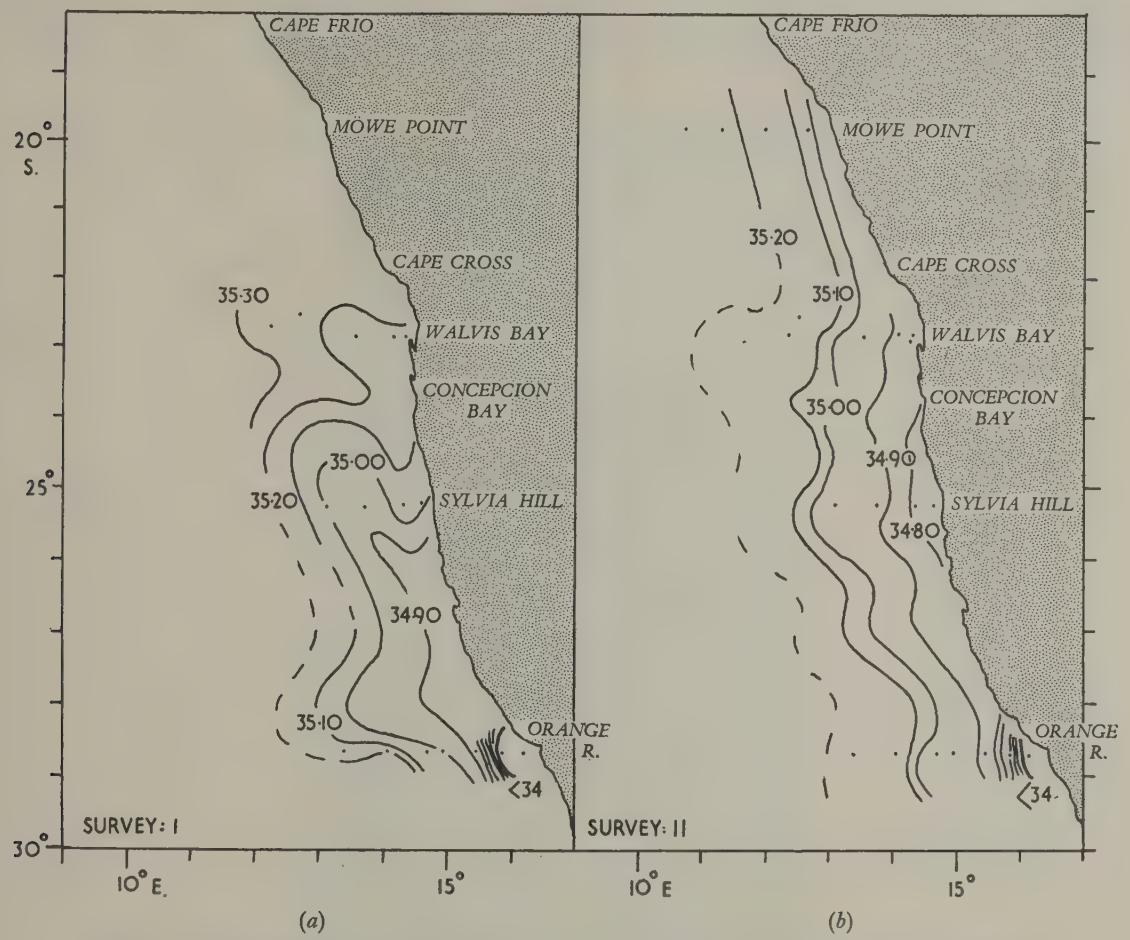

Fig. 8 (*a*). Distribution of surface-salinity (‰), survey I, March 1950. (*b*) Distribution of surface-salinity (‰), survey II, September–October 1950.

this system the cooler and less saline waters lay adjacent to the land, and the warmer, more saline waters farther offshore. Superimposed upon this distribution, however, there was a pronounced series of tongue-like formations within which the cooler coastal waters alternated with intrusions of the warmer oceanic waters lying to the west. Thus the cool waters were not in the form of a continuous belt along the coast, but rather were present as a series of isolated patches extending out from the coast and entering into eddies with the warmer oceanic waters. It will be shown, further, that within these eddies the cooler coastal waters were sharply separated from the warm oceanic surface-waters.

First survey (autumn)

Horizontal distribution of temperature and salinity

On the first survey the lowest surface-temperatures were found in the south of the region, off Paternoster Point (32° 40′ S.) where the lowest recorded was 12·5° C. This cold water, although we have no direct evidence, was probably confined to a fairly narrow coastal strip. In the vicinity of Cape of Good Hope the thermograph readings reached a value of 17° C. only 3 miles offshore, and so there is little likelihood that the cool water extended east of this point.

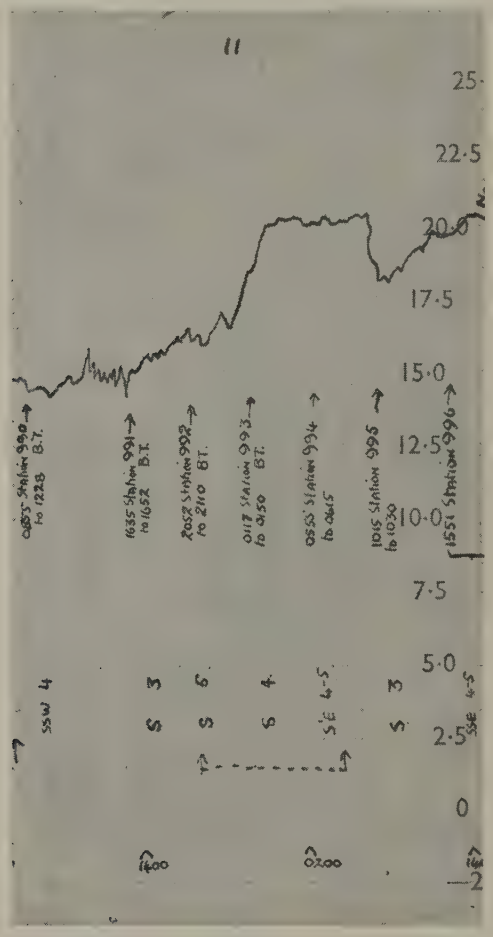

Fig. 9. Photograph of the annotated distant-reading thermograph chart for Saturday, 11 March 1950. Vertical scale, temperature in ° C.

Northwards, towards the Orange river mouth, the extent of cool water became more restricted, and in 29° S. the warmer oceanic water penetrated more closely to the coast. The outflow of fresh water from the Orange river can be detected over a wide area. The surface-salinities at stations in the neighbourhood were vastly reduced (32·39‰ at WS 1001) but the reduction affected only a thin surface-layer, and 50 miles offshore at WS 1000 the surface-salinity was that of the normal sea-water of the region. To the west of station WS 998 the boundary with the warm oceanic water was sharply

defined by a sudden increase in both temperature and salinity (from 18·36° C., 35·01 ‰ to 20·18° C., 35·20‰).

The bathythermograph observations north of WS 996 show that the Orange river line of stations lay along the southern boundary of an extensive wedge of cool water, WS 955 marking its most westerly limit. To the north of this, typical oceanic temperatures were present at WS 994 and 993 but cooler water was again encountered at WS 992. The contouring of the isotherms shows these high surface-temperatures (WS 994, 993) as a tongue of oceanic water converging with the coast, and the strong temperature gradients on either side of it suggest that it was sharply discontinuous with the sur-

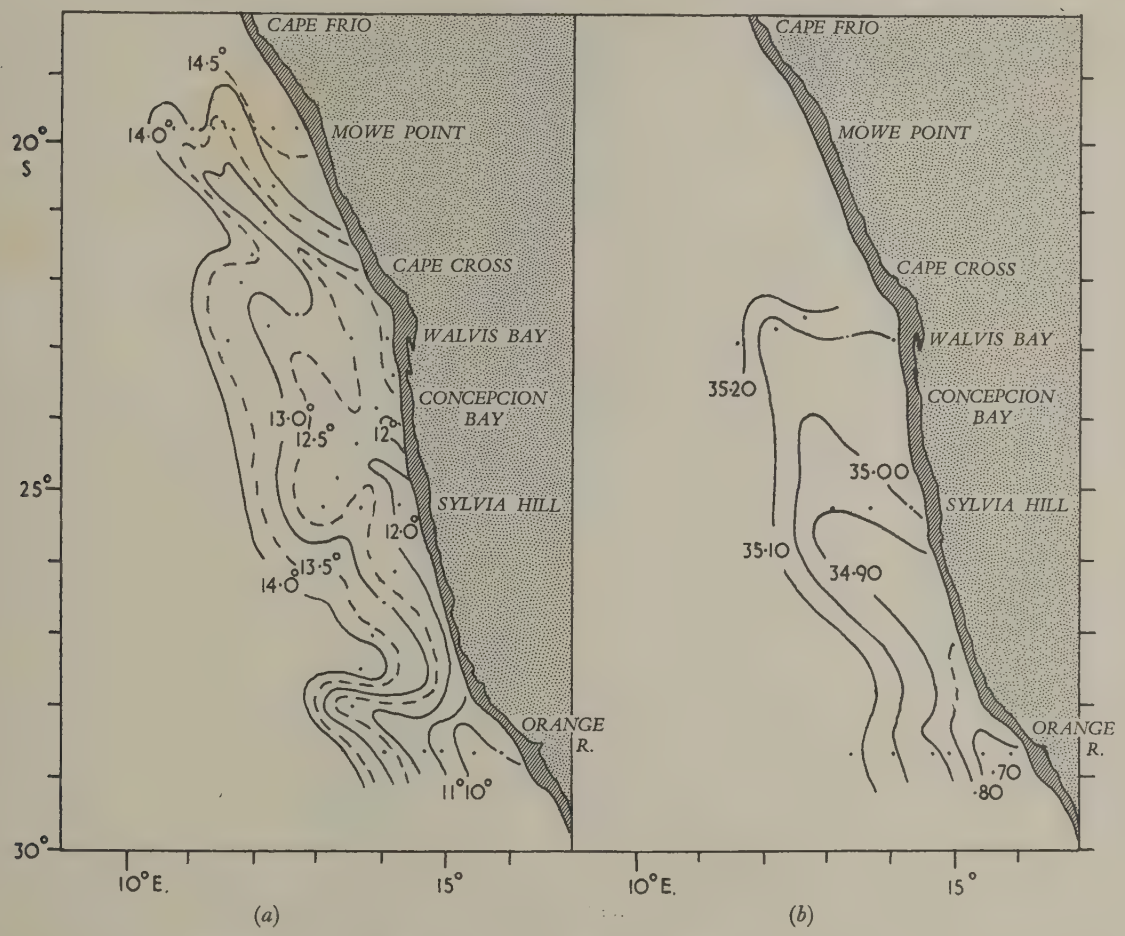

Fig. 10. Distribution of (*a*) temperature, and (*b*) salinity at a depth of 100 m., survey I, March 1950.

rounding cooler water; this is specially noticeable on its northern side, where the temperature fell 3·5° C. in about 15 miles at a distance of 60 miles west of Luderitz Bay (27° S.) (see Fig. 9).

On the next line of stations in 25° S. another such eddy can be defined, but here the oceanic water appeared to extend right in to the coast, causing the cooler water from the south to be displaced seawards. The increase to oceanic temperatures was not evident until WS 986, the westernmost station on the line. It may be that local heating of the surface-waters in the vicinity of station WS 988 had complicated the picture here, but the salinity at WS 988 was higher by 0·06‰ than at the next station seaward, not only at the surface but throughout the water column. A difference in salinity of this order of magnitude may not be significant in itself, but in conjunction with the temperature data

it strongly supports the hypothesis of an offshore influence at this point. Moreover the data to the north of this line also point to the presence of oceanic water converging southwards to this position.

Off Walvis Bay, and to the north of this warm wedge, the water was cooler again, but both the salinities and temperatures are higher than usual for the coastal water, the inshore values of 35·15‰ and 17° C. being more suggestive of some admixture between the two types of surface-water. At the western end of this line of stations, in 23° S., there was again a sudden increase of temperature and salinity into the northern boundary of the warm wedge, with temperatures of over 19° C. and salinities over 35.20‰.

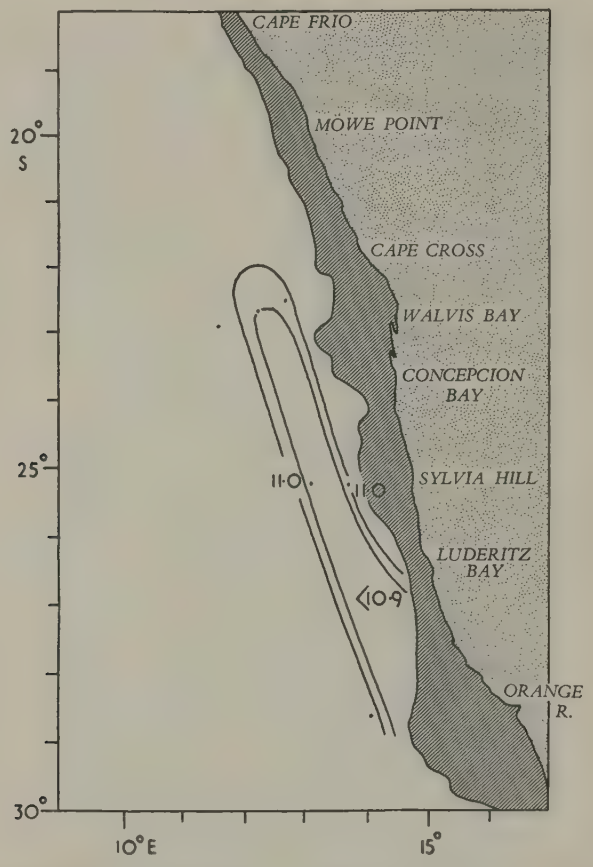

Fig. 11. Distribution of temperature at a depth of 200 m., survey I, March 1950.

To the north of 23° S. the oceanic waters extend in a thin surface-layer apparently pressing towards the coast between 22° and 20° S.

Along the coast the cooler water becomes more and more confined, and eventually to the north of 19° S it appears to converge strongly with the very warm offshore waters (> 22° C.) in a series of eddies about 25 miles from the coast. Finally all trace of it disappears in 16° S., where at 15 miles offshore a temperature of 26° C. was recorded. This whole region between 16° and 19° S. is typical of a convergence region, with very sharp and considerable variations of temperature. Probably the observations demonstrate a compression of the normal convergence between subtropical and tropical surface water, resulting from the presence along the coast of water so abnormally cool for such latitudes. This marked the northern limit of the upwelling region in March 1950.

At a depth of 20 m. the same general characteristics of the surface distribution are to be found, but by 50 m. a change is evident. The disposition of the isotherms and isohalines at these depths represents a transition in varying stages between the surface distribution and that at greater depths. The isotherms and isohalines at 100 m. (Fig. 10) exhibit some more considerable changes which are worthy of note. It will be seen that little change is evident in the Luderitz Bay–Orange river region, (27° to 30° S.) but the cooler coastal water can now be traced more continuously along the coast, and extends to the north in a tongue leaving the coast in the vicinity of Walvis Bay. On the landward flank of this extension warmer water is present, apparently intruding southwards along the coast as far as Concepcion Bay (24° S.). The eddy in 25° S. at stations WS 986 and 987 is still present, and from the north of it another area of low temperatures extends offshore through WS 977, with a markedly lower salinity (35·06‰) than the surrounding water at WS 976 and 978 (35·23‰ and 35·16‰ respectively).

The smaller number of observations made below this depth make it impossible to construct any detailed picture. It is evident, however, that at a depth of 200 m. (Fig. 11) there was an extensive area of cooler water extending N.N.W. from the area between Orange river and Luderitz Bay, the axis of this belt running through WS 986 and 977. Between this tongue and the coast the water was warmer and more saline and suggests a flow from the north along the edge of the continental shelf as far south as Luderitz Bay.

Vertical distribution of temperature and salinity

At most stations there is a layer of almost homogeneous water at the surface, within which the density remains almost constant with depth. This is generally referred to as the convection layer. Throughout the region it is present to a greater or lesser extent, and as a rule it is underlain by a

Table 5. *Depth of the convection layer*

Survey I		*Survey II*		*Survey I*		*Survey II*	
Station	*Depth (m.)*	*Station*	*Depth (m.)*	*Station*	*Depth (m.)*	*Station*	*Depth (m.)*
—	—	WS 1105	0	WS 982	4	WS 1074	10
—	—	WS 1104	0	WS 983	0	WS 1073	30
—	—	WS 1103	10	WS 984	0	WS 1072	30
				WS 985	4	WS 1071	10
WS 964	33	WS 1102	0				
WS 965	41	WS 1101	10	WS 986	0	WS 1070	30
WS 966	30	WS 1100	0	WS 987	0	WS 1069	0
WS 967	10	WS 1099	0	WS 988	0	WS 1064	0
WS 968	18	WS 1098	0	WS 989	0	WS 1063	0
WS 969	25	WS 1097	30				
WS 970	9	WS 1096	0	WS 990	10	WS 1062	0
				WS 991	0	WS 1061	10
WS 971	30	WS 1093	20	WS 992	9	WS 1060	10
WS 972	20	WS 1091	10	WS 993	30	WS 1059	50
WS 973	25	WS 1090	0	WS 994	40	WS 1058	100
WS 974	27	WS 1089	10	WS 995	5	WS 1057	100
WS 975	75	WS 1088	20				
				WS 966	10	WS 1056	50
WS 976	50	WS 1080	75	WS 997	10	WS 1055	50
WS 977	20	WS 1081	75	WS 998	20	WS 1054	30
WS 978	20	WS 1079	50	WS 999	10	WS 1053	10
WS 979	0	WS 1078	20	WS 1000	20	WS 1052	20
WS 980	0	WS 1077	30	WS 1001	0	WS 1051	10
WS 981	0	WS 1075	30	WS 1002	0	WS 1050	0

Where the depth figure '0' occurs, it indicates that the convection layer was either absent or was less than 10 m. in thickness.

strong temperature discontinuity layer, through which the salinity remains almost constant. This discontinuity is therefore a layer of great stability.

The distribution and depth of the convection layer is set out in Table 5, zero indicating where none existed or where it was too thin to be recorded by our observations (< 10m).[1]

Comparing this table with the distribution of surface temperature and salinity (Figs. 7 and 8) it is clear that the convection layer is well developed in the oceanic surface-water, but is notably absent or ill defined in the cooler coastal waters, in which the temperature decreases more steadily from the surface to the sea-bed.

The Orange river line (28° 30′ S.). The vertical sections of temperature and salinity (Figs. 12 and 13) show that both the isotherms and isohalines trend upward to the coast. Although this pattern may suggest an active vertical uplift of water against the coast, such a movement does not appear likely in view of the well-developed discontinuity and the impoverished nature of the surface-waters (fig. 50). The great reduction in salinity of the surface-waters at the inshore stations has already been referred to, and the resulting decrease in density of the surface layers has led to very great stability at these stations.

It is suggested that this section shows an advanced stage of the upwelling process: a relic of previous upwelling rather than a stage of active uplift.

The Sylvia Hill line (25° S.) (Figs. 14 and 15). The whole water column at the inshore stations, WS 988 and 989, was very stable. Clearly there is no indication of inshore upwelling on this line, but then it will be remembered (p. 160) that the inshore stations were apparently influenced by a convergent tongue of oceanic water from the north, and that the cooler water had been displaced offshore. In this cooler water the lower stability and patterns of the isohalines in particular are strongly indicative of vertical motion at stations WS 986 and 987.

The Walvis Bay line (23° S.) (Figs. 16 and 17). The salinity section shows a prominent tongue of highly saline water near the surface. Within this the temperatures are high, and it is characterized by a pronounced thermal discontinuity. This is the northern edge of the intrusion of oceanic water which curves to the south and influences the inshore station on the preceding line. On this Walvis section the discontinuity remains well marked at the inshore stations, and the relatively high temperature and salinity of the latter show that no active upwelling was in evidence. The nature of the inshore water masses here is somewhat problematical, for they appear to exhibit characteristics of a mixture of the oceanic and coastal waters. The most plausible interpretation is that previously upwelled water has subsequently become mixed with oceanic water and the resultant mixture occupies the area in the proximity of the coast at Walvis Bay.

The Möwe Point line (19° 44′ S.). Extending throughout the area to the north of Walvis Bay the oceanic surface-waters form a thin layer about 50 m. deep, overlying a very strong temperature discontinuity. A section through this layer is shown in Fig. 18, which shows the most northern line of stations (the Möwe Point line). It will be seen that on the inshore boundary of this layer the discontinuity weakens and slightly cooler water lies against the coast. Although no salinities were taken in this region it is highly probable that the coastal water is again an admixture of the oceanic and coastal water types. There is a slight indication that the upward trend of the isotherms towards the coast may represent a very early stage of upwelling.

[1] No salinity observations have been available for the 'bathythermograph stations', and so certain assumptions have been necessary. At all full stations the character of the upper layer density distribution, and consequently the convection layer, was primarily dependent upon variations of temperature, and the slight variations of salinity have affected the density curves only slightly. It has therefore been considered justifiable to define the convection layer from the temperature curves at the bathythermograph stations, as the layer within which the temperature remained almost constant.

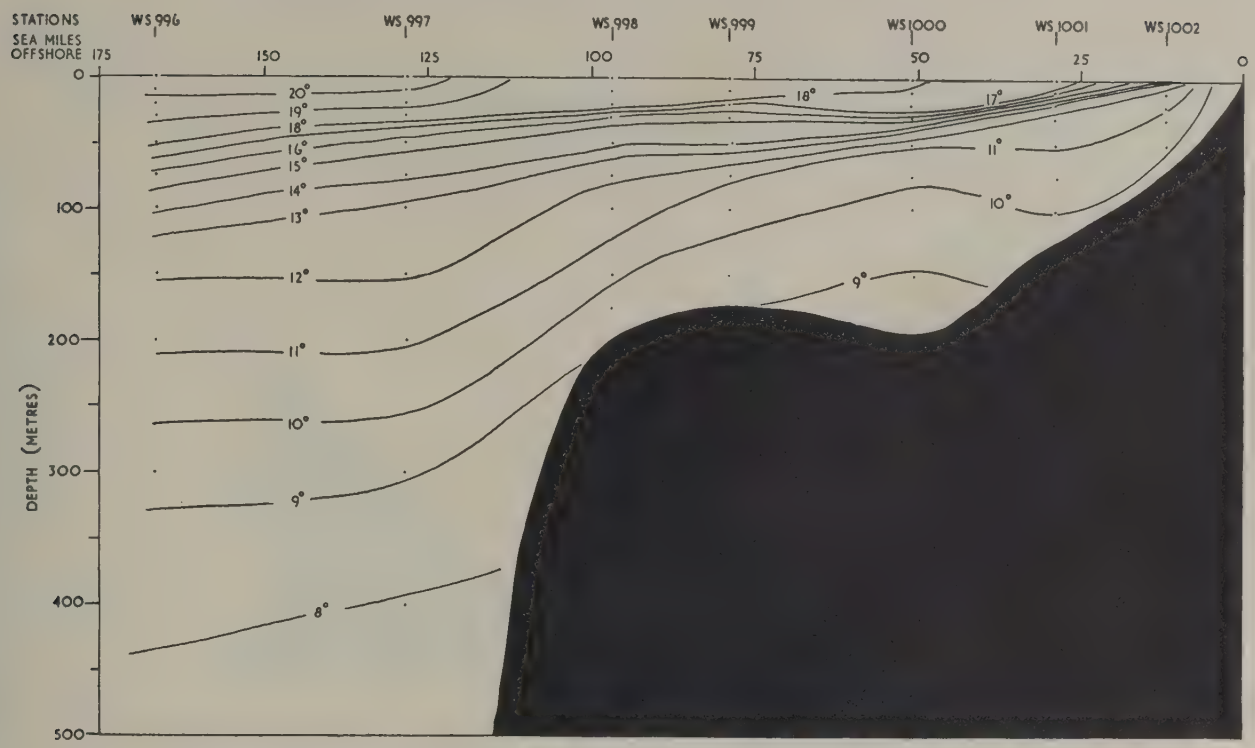

Fig. 12. Distribution of temperature (° C.). Section off the mouth of the Orange river, 12–14 March 1950, survey I. Positions of stations are shown in Fig. 1.

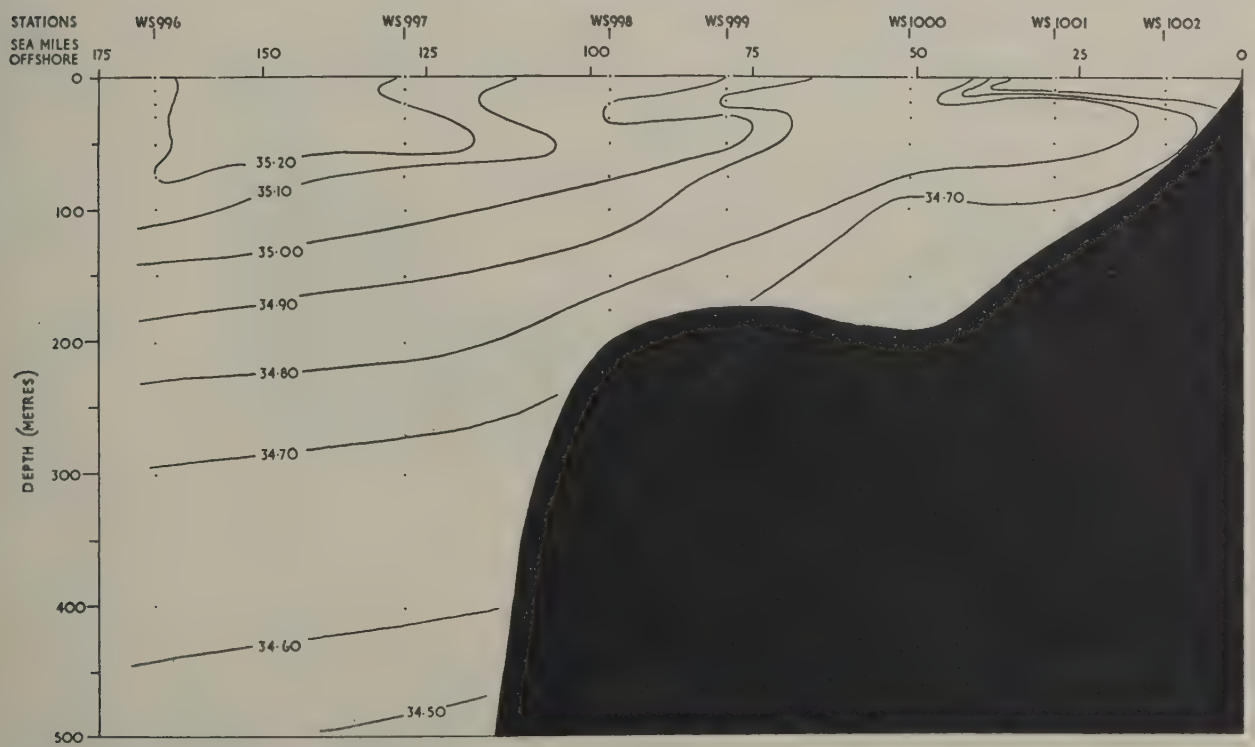

Fig. 13. Distribution of salinity (‰). Section off the mouth of the Orange river, 12–14 March 1950, survey I. Positions of stations are shown in Fig. 1.

At all of the stations below the discontinuity layer the temperature and salinity decrease with depth towards the core of the antarctic intermediate water.

This outline of the conditions on the first survey leads us to the conclusion that, in the region surveyed, two principal types of surface-water can be identified.

(*a*) The coastal or upwelled water, with a low salinity of 35·00‰ or less, and low temperature <18·0° C., and as a rule without any marked convection layer.

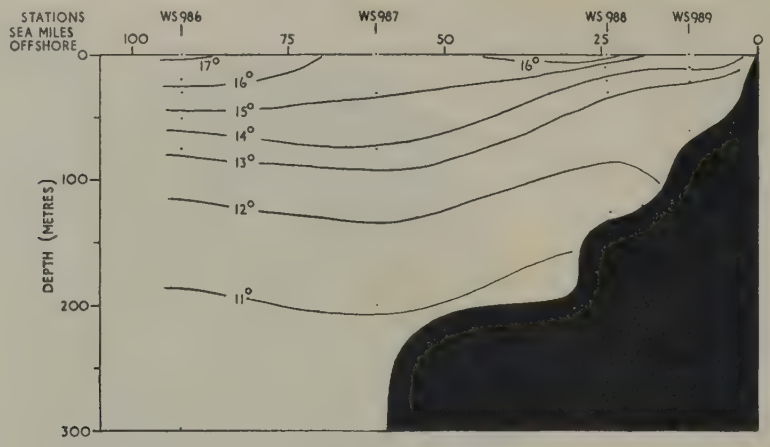

Fig. 14. Distribution of temperature (° C.). Section off Sylvia Hill, 10–11 March 1950, survey I. Positions of the stations are shown in Fig. 1.

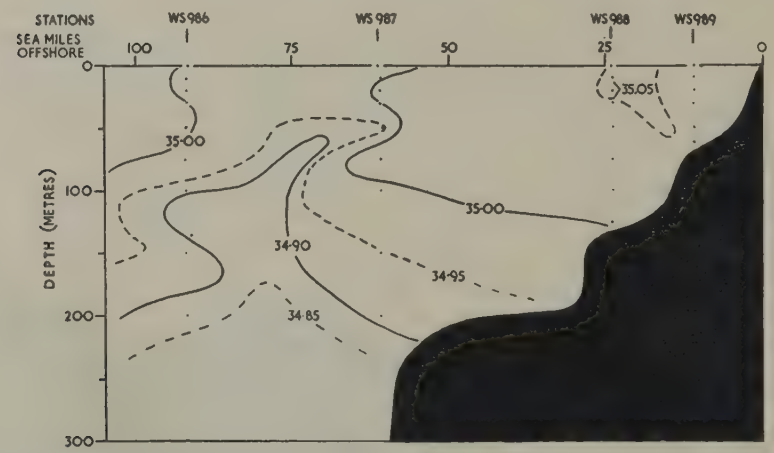

Fig. 15. Distribution of salinity (‰). Section off Sylvia Hill, 10–11 March 1950, survey I. Positions of the stations are shown in Fig. 1.

(*b*) The offshore or oceanic water with a high temperature, usually > 18° C., high salinity > 35·20‰ and a well-developed convection layer.

It is evident that mixtures of these waters occur, as was found in the vicinity of Walvis Bay, but generally they are found sharply distinguished from one another with a pronounced boundary.

There is also evidence of considerable surface heating having affected the coastal waters on survey I, and along with the lack of evidence of active upwelling, this suggests that the conditions throughout the area represent a quiescent state subsequent to previous upwelling.

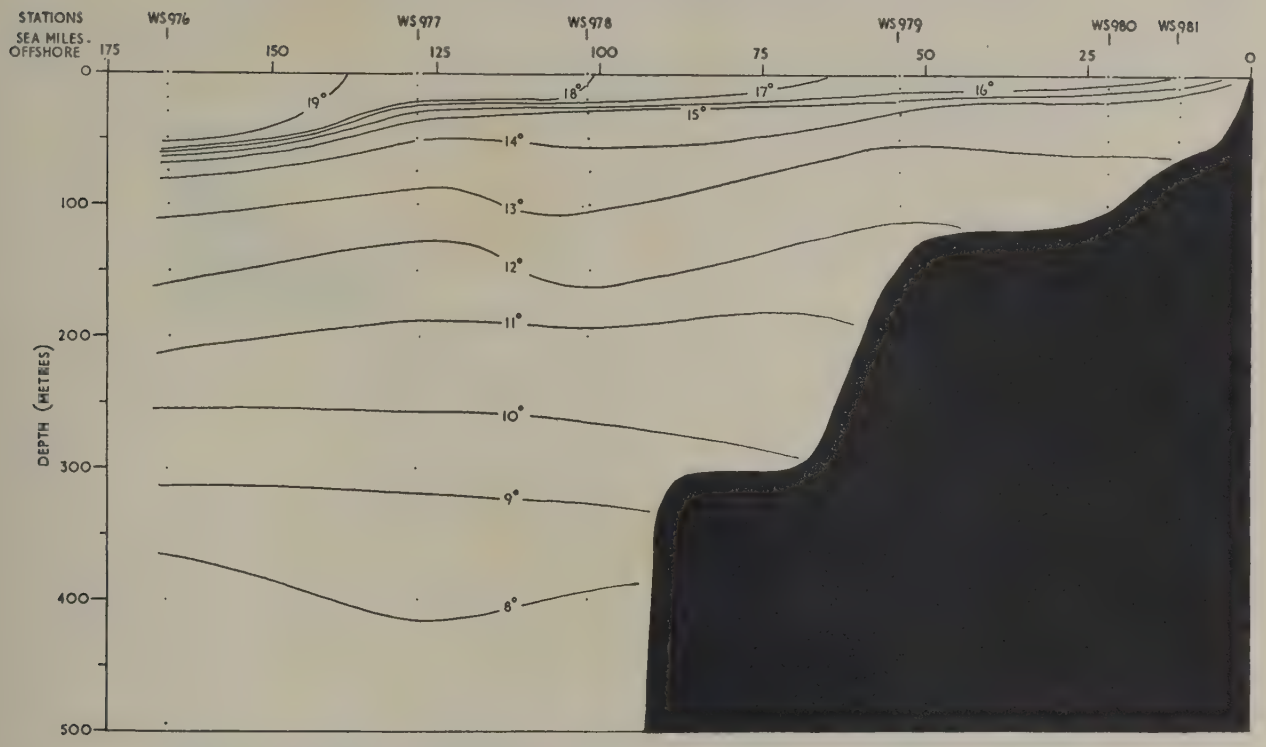

Fig. 16. Distribution of temperature (° C.). Section off Walvis Bay, 6–8 March 1950, survey I.
Positions of stations are shown in Fig. 1.

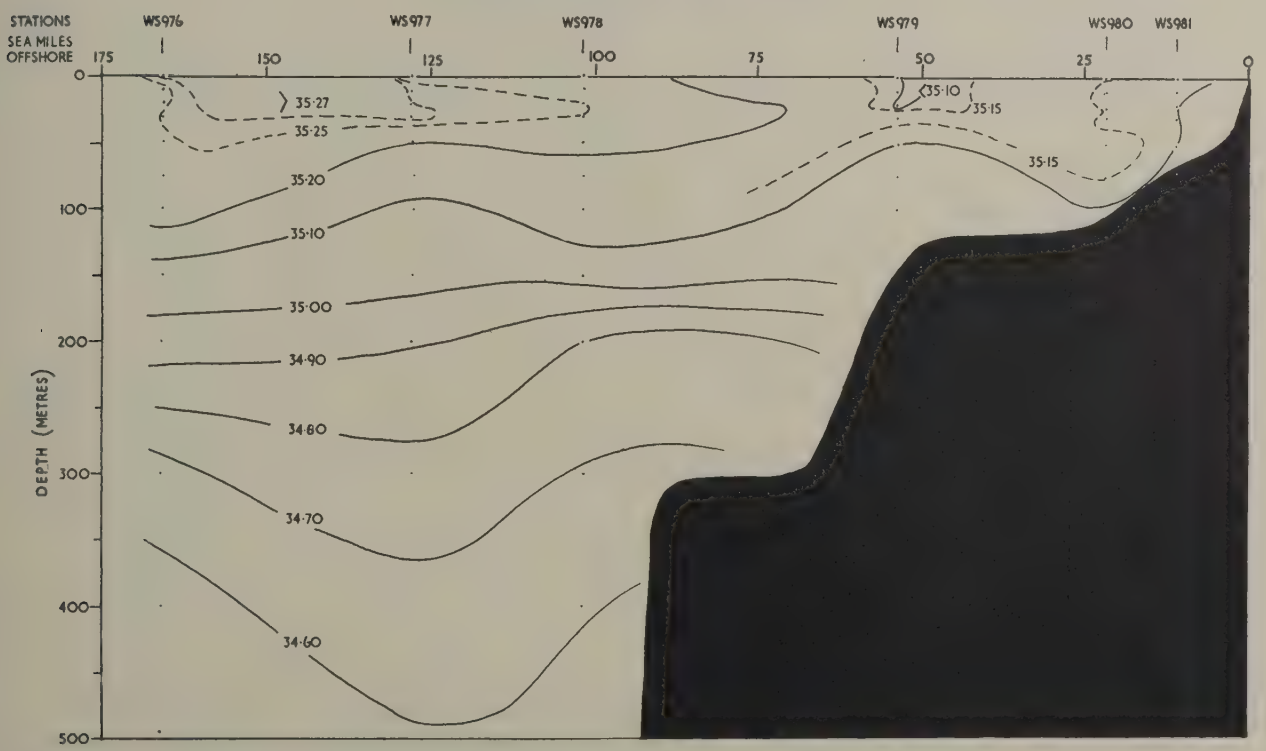

Fig. 17. Distribution of salinity (‰). Section off Walvis Bay, 6–8 March 1950, survey I.
Positions of stations are shown in Fig. 1.

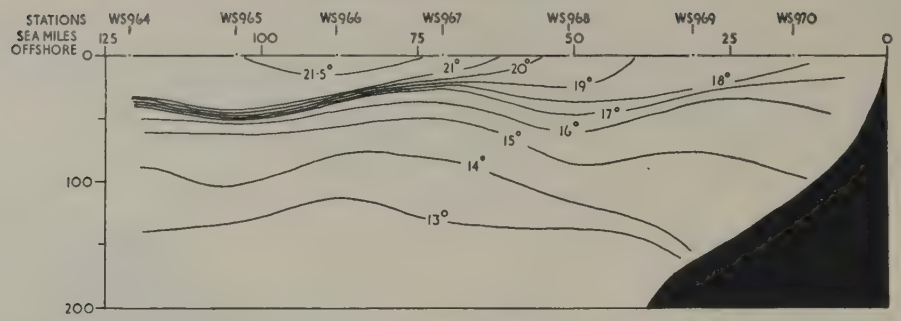

Fig. 18. Distribution of temperature (° C.). Section off Möwe Point, 4–5 March 1950, survey I. Constructed from bathythermograph observations, the positions of which are shown on Fig. 1.

Second survey (spring)

Horizontal distribution of temperature and salinity

On survey II the trend of the surface isotherms and isohalines was similar to that on survey I, but throughout the whole region the temperatures were markedly lower. This can to a large extent be attributed to the seasonal change, survey II having taken place about the coolest time of the year; but also, as will be shown in what follows, the more active upwelling before and during this survey has also contributed to the overall effect.

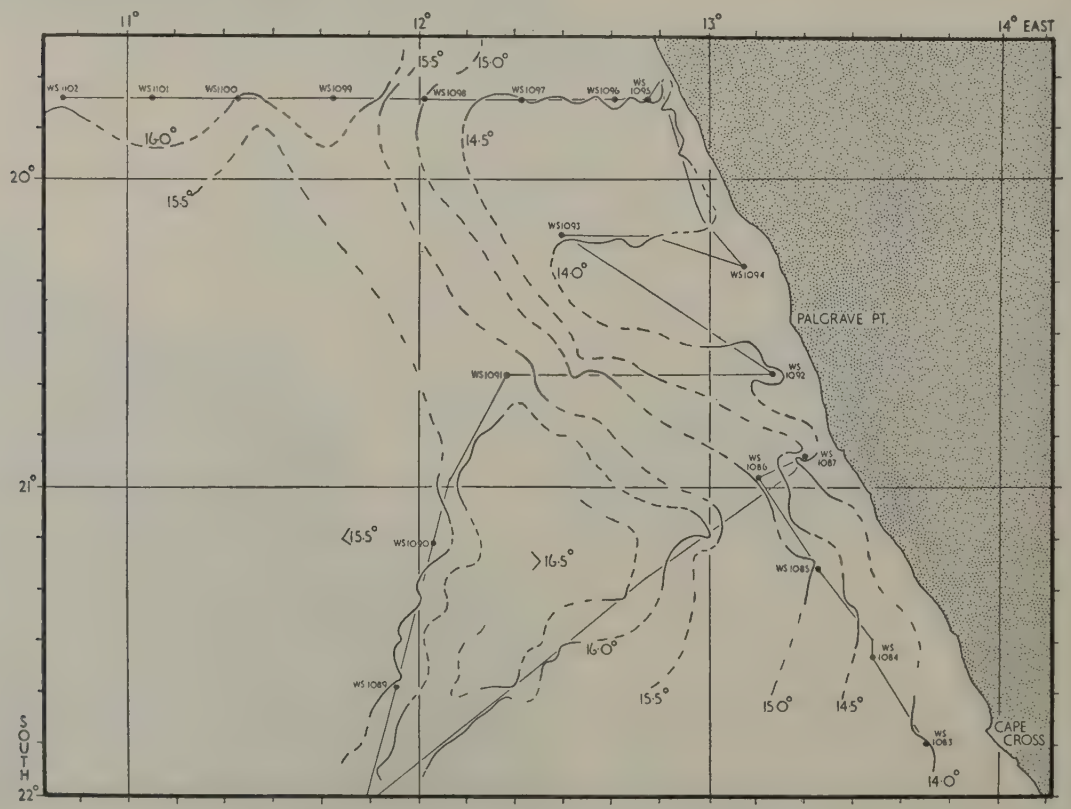

Fig. 19. Distribution of surface-temperature (° C.) between Cape Cross and Möwe Point, survey II, constructed from station observations and distant-reading thermograph records. The track of the ship between stations is shown by the thin line.

The lowest surface-temperature recorded (Fig. 7*b*) was 10° C., off the mouth of the Orange river, but all along the coast as far south as the Cape of Good Hope the temperatures remained below 13° C. In 31° to 32° S. oceanic water with a temperature of 15° C. approached more closely to the coast, but to the north of this the coastal water extended far seawards, forming a broad tongue with its axis extending westwards in 29° S.

In contrast to survey I the Orange river line of stations, which occupied the same positions on both surveys, lay on the northward side of this tongue of colder water. To the north of these stations oceanic water again intruded towards the coast in 28° S. The low salinities in the vicinity of the

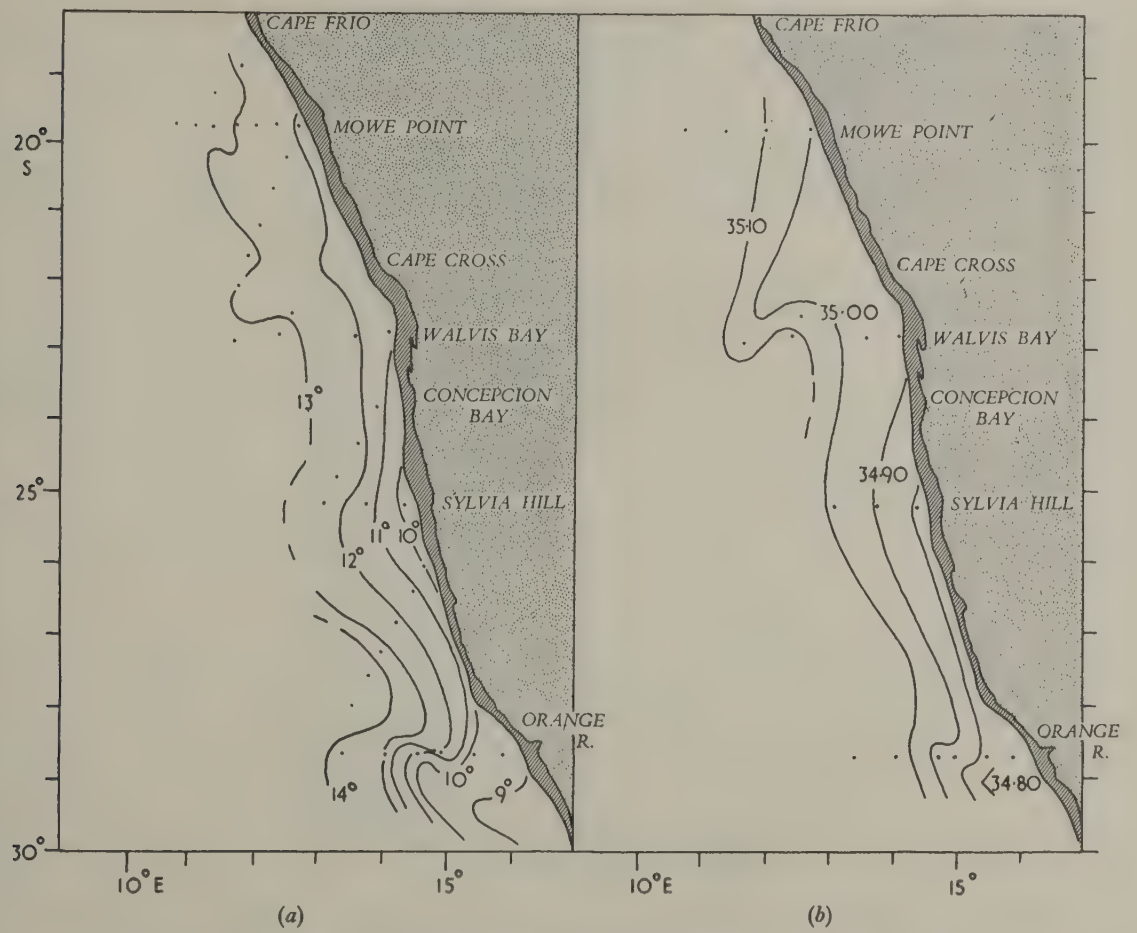

Fig. 20. The distribution of (*a*) temperature (° C.), and (*b*) salinity (‰) at a depth of 100 m. on survey II, September–October 1950.

Orange river mouth were again evident. A sudden increase in salinity between stations WS 1054 and 1055 marked the boundary of coastal and oceanic waters.

Another sharp boundary was traversed between stations WS 1059 and 1060 on the northern side of the oceanic water.

To the north of 27° S. the cooler waters became very extensive, and up to Walvis Bay in 23° S. there was a complex series of small eddies formed by the cooler water, apparently driving offshore in a north-westerly direction. Throughout this area sharp fluctuations of sea temperature were continually encountered, but the temperature remained consistently low.

The stations at the inshore end of the Walvis Bay line all show the typical features of the cool coastal waters, with temperatures of less than 13° C. and salinities of less than 35·00‰. The stations at the offshore end of the line, on the other hand, lying in warmer and more saline water, are characteristic of oceanic conditions. (It should be noted here that the contouring of the isotherms at WS 1079–81 may be open to question for the observations at WS 1079 were taken before, and those at WS 1080 and 1081 after, a considerable gale. As will be shown later (p. 188) this gale produced a considerable alteration in the position of the surface isotherms, and yet no allowance could well be made for this in the general picture).

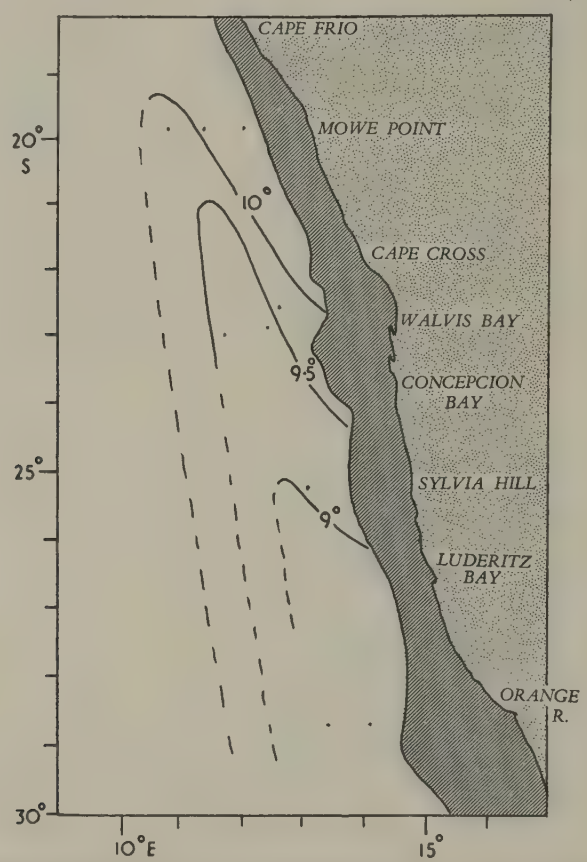

Fig. 21. The distribution of temperature (° C.) at a depth of 300 m. on survey II, September–October 1950.

Between the Walvis Bay line and the Möwe Point line the distribution of surface-temperature is exceedingly complex. From the bathythermograph observations and the records from the distant reading thermograph a more detailed construction of the surface isotherms has been set out in Fig. 19. It will be seen that while the cool coastal water (less than 14° C.) continues along the coast as far as Möwe Point, the temperature rises fairly rapidly offshore to an area of relatively high temperature some 60 miles from the coast. Here the temperature is typically oceanic, reaching a recorded maximum of 16·5° C. This area of high temperature, a patch about 60 miles in diameter, is apparently an isolated feature, for on its western boundary the temperature is again lower (15·5° C.) Several interpretations could be made of this distribution, and unfortunately little guidance can be obtained from the subsurface data, which are only available at the stations. It may be that this phenomenon is solely due

to local surface-heating, but on the other hand the bathythermograph observations definitely suggest, although not conclusively, that this feature is part of an extensive detached eddy between 'oceanic' and 'coastal' types of water. If this interpretation is correct the cooler water outside this warm area would combine to give the eddy an overall diameter of some 120 miles, and extending in depth to 50 m.

At Cape Frio, in 18° 30′ S., a temperature of 15·1° C. was recorded about 7 miles offshore, but north of this yet another patch of cooler water was present, extending up to the Cunene river mouth. From there northwards, however, the temperature of the surface-waters increased steadily, until in 14° S. the tropical boundary was encountered and the temperature increased rapidly to values over 22° C.

The distribution of temperature and salinity at a depth of 100 m. (Fig. 20) has the same general characteristics as that at the surface, the cooler and less saline waters lying uniformly along the coast, with the warmer more saline waters offshore. Although the smaller number of observations at this depth are probably responsible for the smoothing out of the isotherms and isohalines, they still show up quite clearly the pronounced eddy in the vicinity of the Orange river. The regions of lowest temperature and salinity as shown by the 10·0° C. and 34·80‰ isolines are present to the south of the Orange river and off Luderitz Bay.

At 150 m. an entirely different pattern appears. This is not illustrated but along with the distribution at 200 m. it represents a transition to the distribution at 300 m. (Fig. 21). At 300 m., in spite of the paucity of observations, it is possible to recognize that the distribution is roughly similar to that at a depth of 200 m. on survey I. Here we find an apparently anomalous situation with the warmer and more saline water nearest to the coast while the cooler water lies further offshore. There can be no doubt that further to the west warmer water must have been present, and so it seems that on this survey the cooler water at this depth must have been still more extensive and further displaced from the shore than on survey I. This was concurrent with an increase in the current of warmer water which runs south along the coast.

Vertical distribution of temperature and salinity

An outstanding feature of the second survey in comparison with the first is the absence of the very strong thermoclines which were found so frequently in March. At most stations, particularly those in the offshore waters, there is a convection layer on the surface, and below this the temperature and salinity decrease gradually into the deeper water. In several places where a well-defined convection layer had apparently been present, surface heating has reduced the density and produced a thin stable surface layer. The depth distribution of the convection layer on survey II is shown in Table 5.

The Orange river line (28° 30′ S.). The low surface salinities inshore are a result of the fresh-water inflow of the river, and they have produced a very stable surface layer at station WS 1050. Further offshore, however, at WS 1051 a thin convection layer is present, and this deepens and becomes more pronounced farther to the west. The vertical sections of temperature and salinity (Figs. 22 and 23) contrast vividly with the conditions in March. The marked upward slope of the isotherms and isohalines towards the coast, combined with the active offshore transport of surface-water as suggested by the salinity section, shows most clearly the characteristics of active upwelling. It will also be seen that the isotherms and isohalines, while approaching the surface inshore, also rise towards the surface in the proximity of the edge of the continental shelf. There seems to be clear indication, therefore, of an additional divergent movement in this position. As will be shown later, this is probably associated with the mechanism of the process of the upwelling.

North of the Orange river line the tongue of warm offshore water at WS 1057 and 1058 has an almost constant temperature in the upper 100 m. A relatively sharp boundary was present on the

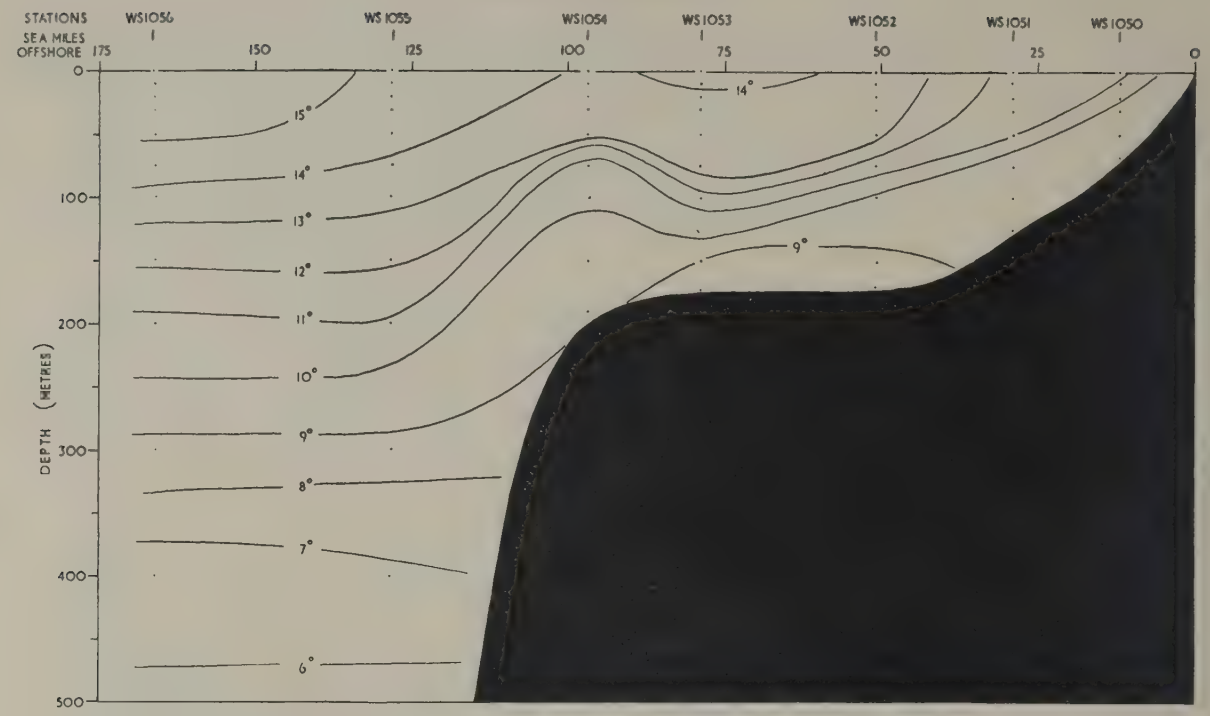

Fig. 22. Distribution of temperature (° C.). Section off the mouth of the Orange river, 21–24 September 1950, survey II. Positions of the stations are shown in Fig. 2.

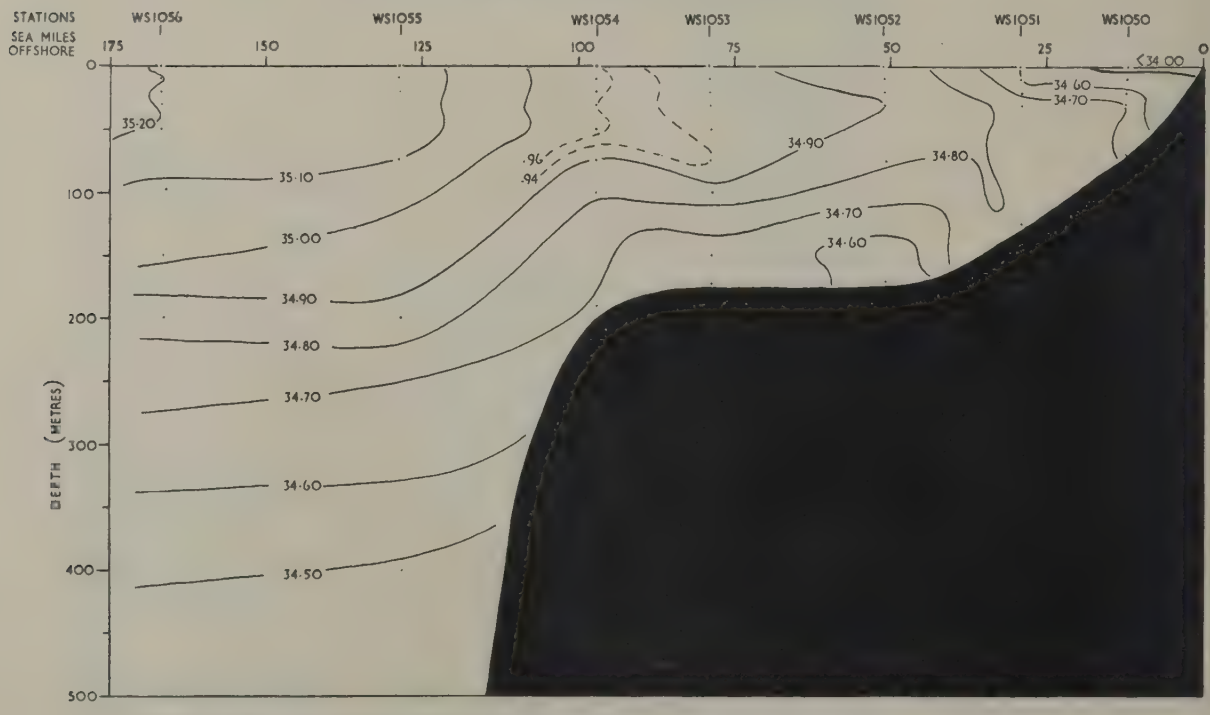

Fig. 23. Distribution of salinity (‰). Section off the mouth of the Orange river, 21–24 September 1950, survey II. Positions of the stations are shown in Fig. 2.

northern side of this wedge, where it abutted on the cooler coastal water. At stations WS 1061 and 1062 a slight temperature inversion was revealed by the bathythermograph observations, at depths of 105 and 75 m. respectively (Fig. 24).

The Sylvia Hill line (25° S.). Stations WS 1063–70 did not lie sufficiently far to the west to reach the boundary with oceanic water, and consequently they all lie within the coastal water. The vertical sections (Figs. 25 and 26) show that active upwelling must have been taking place on this line.

The Walvis Bay line (23° S.). Here again there are indications of active upwelling (Figs. 27 and 28). The inshore waters show an interesting point: the salinity of the inshore surface-water is very low (34·84‰) and remained low out to WS 1078 (34·96‰). Below this, however, the salinity increased to 34·97‰ on the sea bed of the continental shelf.

The salinity section suggests that there is a pronounced uplift of deeper water taking place on the edge of the continental

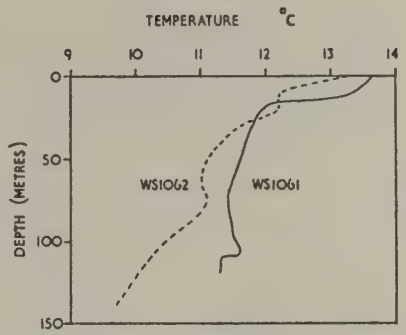

Fig. 24. Graph of temperature (° C.) against depth (metres) at stations WS 1061 and 1062, showing inversions present at these stations.

Fig. 25. Distributions of temperature (° C.). Section off Sylvia Hill, 25–27 September 1950, survey II. Positions of the stations are shown in Fig. 2.

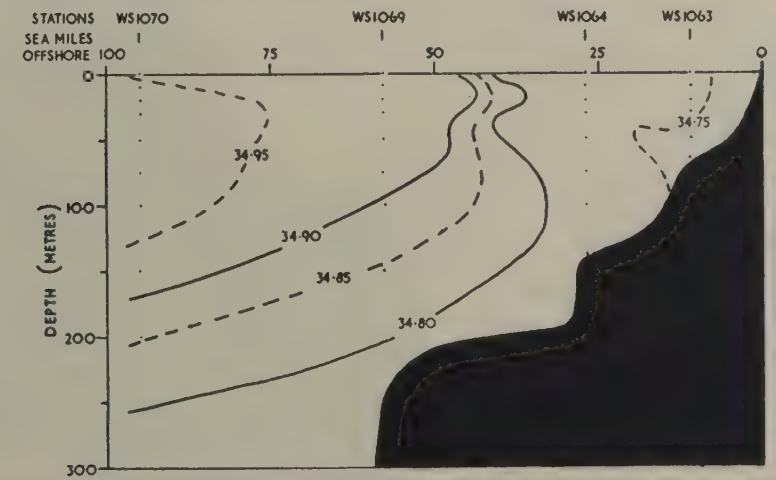

Fig. 26. Distribution of salinity (‰). Section off Sylvia Hill, 25–27 September 1950, survey II. Positions of the stations are shown in Fig. 2.

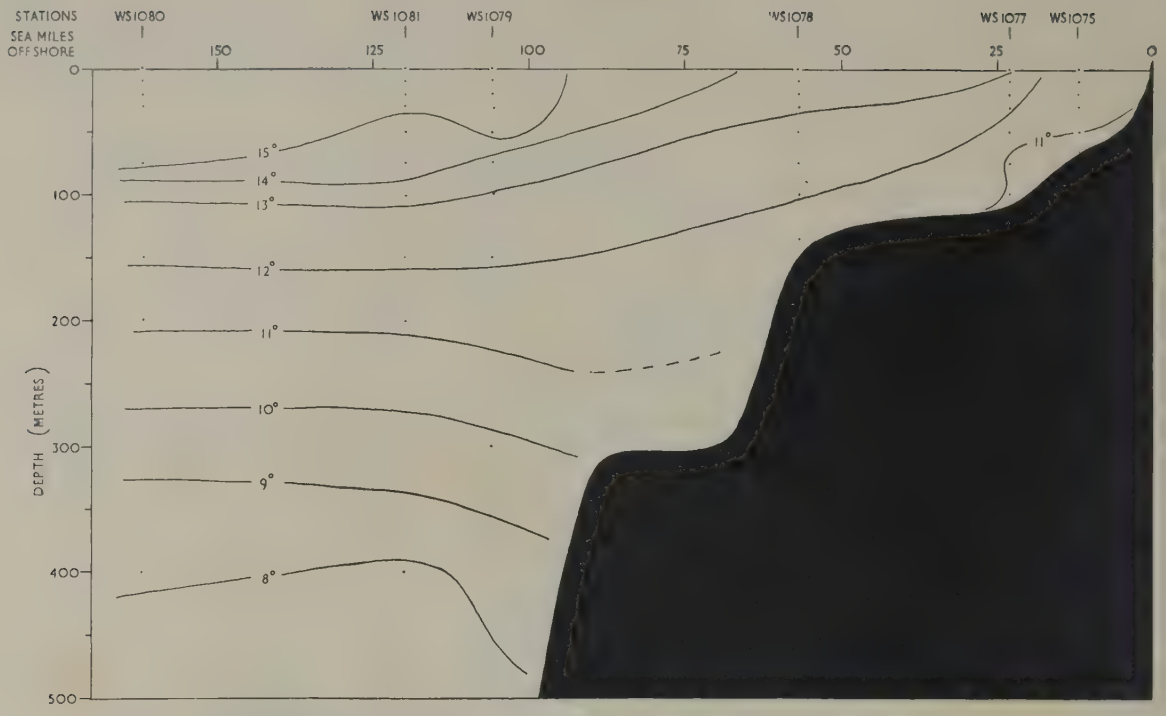

Fig. 27. Distribution of temperature (° C.). Section off Walvis Bay, 29 September–3 October 1950, survey II. Positions of the stations are shown in Fig. 2.

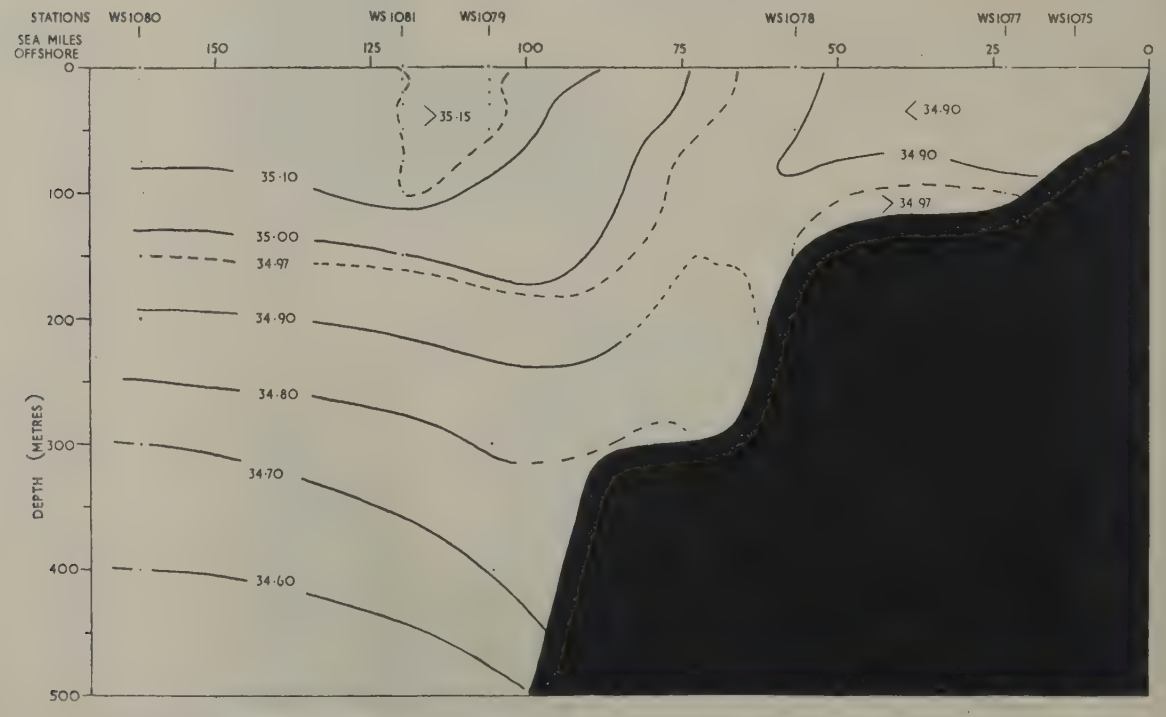

Fig. 28. Distribution of salinity (‰). Section off Walvis Bay, 29 September–3 October 1950, survey II. Positions of the stations are shown in Fig. 2.

shelf, and that the low salinity of the surface-layers inshore must be connected with this movement, but it is difficult to interpret the significance of such a movement.

The lack of any salinity observation in the region of the large eddy between the Walvis Bay line and the Möwe Point line prevents us from drawing any conclusion about the structure and movement of these waters.

The Möwe Point line (19° 44′ S.) (Figs. 29 and 30). Throughout the greater part of this line the

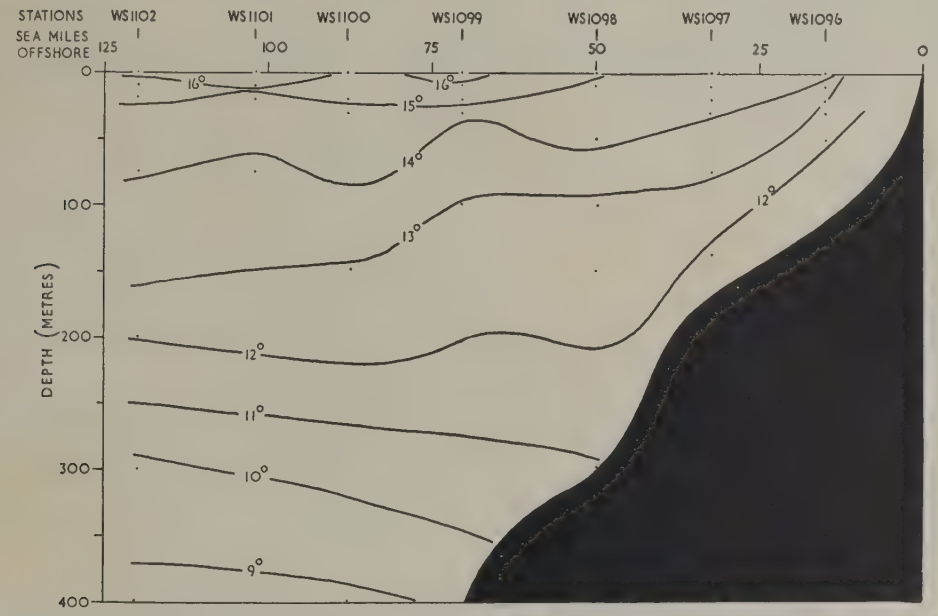

Fig. 29. Distribution of temperature (° C.). Section off Möwe Point, 9–11 October 1950, survey II. Positions of the stations are shown in Fig. 2.

Fig. 30. Distribution of salinity (‰). Section off Möwe Point, 9–11 October 1950, survey II. Positions of the stations are shown in Fig. 2.

highly saline water at the surface, bounded both inshore and offshore by water of lower salinity, shows that the stations have sectioned the northern edge of oceanic surface-water which was involved in the large eddy lying south of this line. The isotherms and isohalines both slope upwards towards the coast at the inshore stations, but this does not necessarily mean that active upwelling was taking place. The same effect could be created by the presence of the oceanic water so close to the coast, compressing the coastal type of water into a narrow strip adjacent to the land. The salinity and temperature distribution in such a strip of water would then necessarily, on account of the laws governing the density distribution, resemble the pattern created by upwelling.

The isolation of this inshore water from the deeper water, apparent in the salinity section (Fig. 30), suggests that active upwelling was not taking place.

To the north of this section another centre of upwelling may have been present at Cape Frio (see Fig. 7*b*) in 18° 30′ S., but there are insufficient data to decide this question.

To sum up, it is evident that the same essential features were present on both of these surveys. On the second survey we can distinguish the same two types of surface water.

(*a*) The coastal or upwelled water, which on survey II is characterized by temperatures below 14·0° C. and salinities of less than 35·00‰. The convection layer in this water is better developed than on survey I, but the underlying discontinuities are not so pronounced. These differences must be caused by the stronger winds and upwelling on survey II.

(*b*) The offshore water, characterized by temperature over 14·0° C. and salinities of over 35·10‰. This is in general cooler, but very similar in other respects to the same type of water on survey I.

In survey II, active upwelling was found on the two southern sections, and possibly also on the Walvis Bay line, while only on the northernmost section (the Möwe Point line) were quiescent conditions encountered.

Table 6. *Stability of the* 0–50 m. *and* 0–100 m. *layers*

Survey I			*Survey II*		
	$10^5\, d\sigma t/dz$			$10^5\, d\sigma t/dz$	
Station	*0–50 m.*	*0–100 m.*	*Station*	*0–50 m.*	*0–100 m.*
WS 976	−63	845	WS 1102	975	743
WS 977	2000	1453	WS 1100	675	550
WS 978	2113	1535	WS 1098	500	495
WS 979	1825	1297	WS 1096	1213	855
WS 980	2050	1387			
WS 981	1775	—	WS 1080	63	268
			WS 1081	388	478
WS 986	1088	992	WS 1079	38	258
WS 987	475	577	WS 1078	175	230
WS 988	1825	1237	WS 1077	638	538
WS 989	1100	—	WS 1075	150	—
WS 996	875	1257	WS 1070	163	262
WS 997	1850	1413	WS 1069	375	370
WS 998	1900	1540	WS 1064	438	305
WS 999	2138	1778	WS 1063	500	—
WS 1000	2375	817			
WS 1001	7688	5145	WS 1056	83	162
WS 1002	4075	—	WS 1055	63	138
			WS 1054	275	503
			WS 1053	250	387
			WS 1052	200	447
			WS 1051	650	617
			WS 1050	2450	—

Stability of the water masses

To obtain some further comparison of the characteristics of the upper water layers on the two surveys the vertical stability of the water columns has been determined. This has been calculated approximately as $10^5\, d\sigma t/dz$ for the layers 0–50 m. and 0–100 m., and is set out in Table 6.

In spite of the instability of the water at WS 976 the great stability of the upper 50 m. at all the other stations on survey I contrasts most vividly with the generally lower stability on survey II. This pronounced difference, the whole region being some ten times more stable in the upper 50 m. on the first than on the second survey, reflects clearly the difference in the meteorological conditions on the two surveys.

THE WATER MASSES

Water masses of the South Atlantic

Wüst (1935) plotted T-S curves for three more or less meridional lines of 'Meteor' stations in the Atlantic Ocean. The remarkable similarity of these curves within the South Atlantic is at once apparent from his diagram (his p. 216). Excepting the upper layers where external factors come into play, the curves all fall within a regular pattern. A typical T-S curve for the South-east Atlantic is shown in Fig. 31.

The 'Bottom' water is a cold dense mass of water lying in the deeper basins. It originates in the Antarctic, where cooling processes in the proximity of the continent cause the water there to sink down the continental slope, and being very dense it spreads out across the ocean floor. The main centre of this sinking appears to be the Weddell Sea, but it probably also occurs at other points along the Antarctic coast. The water thus formed can be traced by its low temperature and salinity, and it describes a northward flow into the South Atlantic. Partly under the influence of the earth's rotation, but probably mainly owing to the bottom topography, the principal flow takes place up the western side of the South Atlantic. A certain amount of the water flows up into the Cape Basin, but this does not go far north since its passage is interrupted by the Walvis Ridge, a connecting ridge between the African continent and the Central Atlantic Ridge. Wüst (1935) demonstrated that the potential temperature of the bottom water south of the Walvis Ridge was about 1° C. lower than that to the north of the ridge where it was over 2° C. He suggests that the flow up the western side of the ocean infiltrates in a cyclonic movement through a gap in the Central Atlantic Ridge (the Romanche gap) and enters the Angola Basin from the north.

Lying above the bottom water, and extending up to nearly 1000 m. from the surface, there lies a great mass of water called the 'North Atlantic deep water'. Owing to its great homogeneity it occupies relatively little space on the T-S diagram (Fig. 31), the observations within it being clustered around an intermediate *maximum* of salinity. Taking other factors into account, however, Wust has shown that the deep water is, in actual fact, composed of three separate layers. As far as we are concerned the three deep water layers can all be taken together, and considered as having a general southward flow. The water leaving the North Atlantic does so principally on the western side, so that the best-defined flow in the South Atlantic is found down the South American coast, the movement in the eastern part of the ocean being much less well defined. On reaching higher latitudes the whole mass of deep water becomes directed to the east.

Above the deep water, there is a layer of minimum salinity. This characterizes the main axis of northward flow of the 'Antarctic intermediate water'. Formed by the sinking of antarctic surface-water, from the antarctic convergence in about 50° S., this layer moves northward at a depth of between 600 and 800 m. Again the strongest movement is on the western side of the ocean, and indeed

in the eastern South Atlantic there seems to be a tendency to an eastward movement, particularly in the Gulf of Guinea, where it apparently diverges cyclonically from the main northerly trend. Thus in the South-west African region the flow is again ill defined.

In the subtropical region between the surface-waters, and the salinity minimum of the antarctic intermediate water the T-S curves follow a nearly straight line relationship to within about 200 m. of the surface, above which the circulation becomes more complex within the tropical and subtropical surface and subsurface layers. This water mass, represented by the nearly straight line part of the curve, has been termed the 'South Atlantic central water' (Sverdrup, Johnson and Fleming, 1946). The process of its formation is still rather obscure. Sverdrup *et al.* (1946) suggest that it is probably formed by a simple process of sinking along surfaces of equal density in the region of the subtropical convergence, as the *vertical* T-S relationship of the South Atlantic

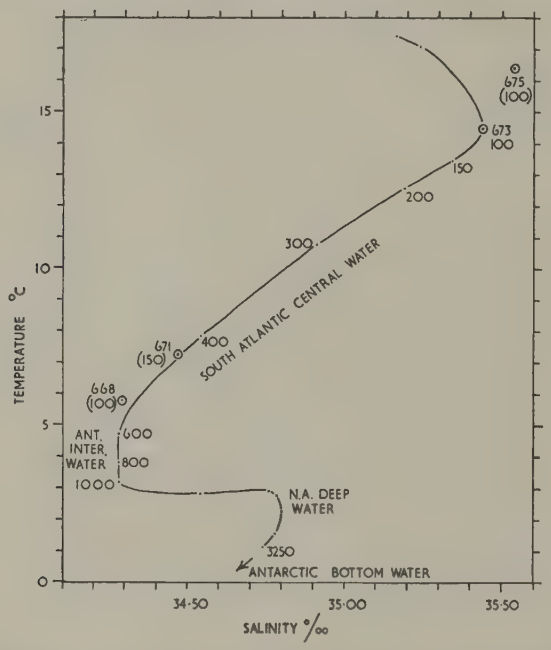

Fig. 31. A typical temperature–salinity curve for the south-east Atlantic, drawn from observations at 'Discovery' station 673. The water masses represented on the curve are named. The additional points in open circles are the T–S relationships at the stations (675, 671 and 668) at the depths (in brackets) shown. These stations lie in a north–south line across the subtropical convergence, so the points show the horizontal T–S relationships at subsurface depths across this region, indicating the close similarity to the vertical T–S curve for the South Atlantic central water. Depths are in metres.

central water corresponds closely with the *horizontal* T-S relationship in the subtropical convergence region (see Fig. 31). Clowes (1950), however, has taken exception to this view on the grounds that an examination of the surface T-S relationships in the region 0° to 20° E. and 30° to 40° S. fails to show any similarity to the vertical T-S curve of the South Atlantic central water. He considers that a more likely explanation is a direct mixing between the antarctic intermediate water and the subtropical surface- and subsurface waters, which would probably take place in the region of the subtropical convergence.

North of the antarctic convergence in about 50° S., where the antarctic surface-water sinks to form the intermediate water, there lies a belt of warmer water, the subantarctic water, whose characteristics suggest that it is a mixture of antarctic water and warmer water from the north. Extending north-

wards to the subtropical convergence, a distance of about 600 miles, this is a relatively shallow layer. Under a well-mixed surface-layer, which is rather poorly saline, there is a pronounced subsurface salinity maximum, and below this again the water becomes less saline.

It seems fairly certain (Deacon, 1936) that this subsurface salinity maximum represents the core of a southward flow within the subantarctic zone. The properties of this water suggest that it is replenished from two sources, from a subsurface highly saline current within the subtropical zone itself, and (to a lesser extent) from subantarctic water sinking at the subtropical convergence and returning to the south. The vertical T-S curve below the subtropical convergence suggests that the central water there is a mixture between water of higher salinity than the surface-water and the antarctic intermediate water (see Fig. 31), showing that it is probably the subsurface current which is involved in the mixture in this region. The subsurface salinity maximum is not generally distributed over the ocean, however, and no doubt elsewhere it is the surface-water which mixes with the intermediate water as occurs in the subtropical region itself.

Above the salinity maximum where present, and generally over the subtropical zone, the surface water is a fairly homogeneous layer, and its movements, governed principally by the trade winds, follow an anti-cyclonic pattern. From the Brazil current flowing southwards down the western side of the South Atlantic, the water is carried to the east with a decreasing southerly component. It appears to be the balanced effect of this movement with the northward drift of the subantarctic surface-water which is responsible for the maintenance of a sharp subtropical convergence. Deacon has already pointed out that there is not much likelihood of this water sinking at the subtropical convergence, and it is probably mostly carried east in a direction more or less parallel to the convergence. As it reaches the eastern side of the ocean, it turns more to the north, and, with perhaps a contribution from the Agulhas current (Dietrich, 1935*a*, *b*), it returns up the eastern side of the Atlantic as the South-east trade wind drift. Across the Atlantic, and forming a line approximately from Angola to Rio, about the 23° C. surface isotherm, there is a convergence of the surface-water, and to the north of this line there is a warm highly saline layer which is very poor in nutrients and sharply divided from the underlying water by a strong discontinuity layer. This is the tropical surface-water, which owes its existence to the immense amount of heating and evaporation in this region. From the African side the south equatorial current carries this water across the Atlantic to Brazil, somewhat in the form of a left-hand screw. Within itself the layer is homogeneous and well mixed.

Temperature-salinity relationships of the South-west African waters

The typical T-S curve for the offshore stations of the 'William Scoresby' is very similar to the general pattern described for the South Atlantic.

None of the 'William Scoresby' stations was in deep enough waters to encounter the Antarctic bottom water which the 'Meteor' observations showed to fill the depths of the Cape Basin, but at all stations of sufficient depth off the continental slope the North Atlantic deep water was encountered. At WS 976 only, a maximum salinity of 34·91 ‰ at 2420 m. was recorded. This represented the nearest observation to the core of the upper deep water, but at all other stations salinity values around 34·80 ‰, and still increasing at the lowest depths of observation, indicated that the central core of the upper deep water had not been reached.

Sometimes between the southward flow of the North Atlantic deep water and the northward flow of antarctic intermediate water, a slight temperature inversion is produced, such as was recorded at station WS 996 where the water at 1470 m. with a temperature of 3·05° C. was 0·04° C. warmer than the water at 1170 m. Deacon has recognized this layer of minimum temperature, but considers that

the flow of the intermediate current is principally in the layer of minimum salinity, and that its flow in the layer of minimum temperature is probably much affected by turbulent mixing with the underlying deep water.

A well-marked layer of minimum salinity was encountered at all stations off the continental shelf on both of the surveys. Table 7 shows the depths and observed salinities in the layer of minimum salinity. Wüst developed a method for studying the mixing path of a water type from its T-S relationships. Initially the water type is plotted as a point on a T-S diagram. As it mixes with adjacent layers

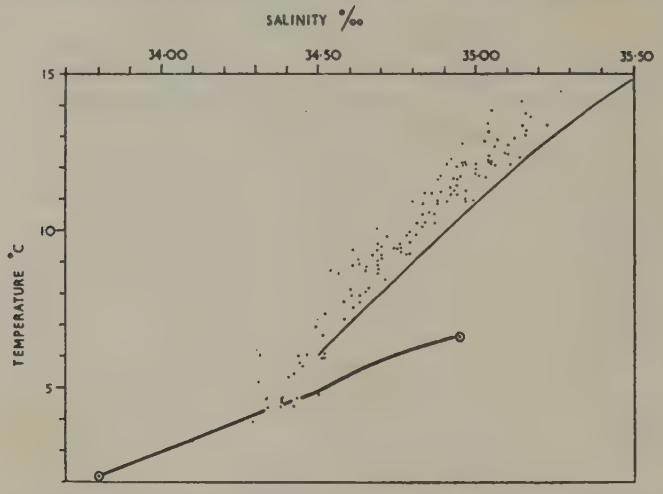

Fig. 32. Temperature-salinity relationships of the water layers between 100 m. and the salinity minimum of the Antarctic intermediate water. The heavy line shows the relationship in the core of the Antarctic intermediate water from its source (left) to its northern limit (right), after Wüst, 1935. The thin line is the line characteristic of South Atlantic central water (Sverdrup, 1946).

the point moves along a line, until eventually its characteristic, say a salinity minimum, disappears (Fig. 32). Thus one can follow the water type from its beginning until it is completely obliterated by mixing with other waters. This method is known as the 'Kernschichte methode'—the core method. Applying it to the intermediate water one finds that in the core of the antarctic intermediate layer the effect of vertical mixing has altered the T-S relationship from the original water type (T = 2·2° C., S = 33·80‰) to a value of T = 4·7° C., S = 34·4‰ off South-west Africa (Fig. 32). As the salinity

Table 7. *Salinity minima in the antarctic intermediate layer*

Station	*Salinity minimum* (‰)	*Depth* (*m.*)
WS 976	34·50	700
WS 977	34·34	820
WS 978	34·45	600
WS 986	34·38	800
WS 996	34·34	600
WS 997	34·31	570
WS 1056	34·33	600
WS 1070	34·42	600, 820
WS 1080	34·38	780
WS 1081	34·29	990
WS 1102	34·31	630

The figures show the minimum values of salinity recorded at 'William Scoresby' stations, and the depths of the observations.

minimum finally disappears at T = 6·6° C., S = 34·95‰ in about 15° N., so we can consider that the antarctic intermediate layer off South-west Africa contains only about 50% of the original water type.

Above the antarctic intermediate water core, and to within 100 m. of the surface, all the 'William Scoresby' observations fall fairly close to a nearly straight line joining the points T = 14·0° C., S = 35·20‰ and T = 4·7° C., S = 34·40‰. It will be seen that this line lies somewhat to the left of Sverdrup's curve for the South Atlantic central water (Fig. 32) (Sverdrup *et al.* 1946), but it should be remembered that Sverdrup has taken a mean curve for the whole South Atlantic.

Above 100 m. external influences come into play and the water becomes subjected to heating, cooling, evaporation, etc., and these account for the more widely spaced distribution of the T-S points. But the effect of these external influences is fairly well defined and with caution it is possible to derive at least some information concerning the surface water-layers from their T-S relationships.

Water masses of the upper layers (0–200 m.)

Oceanic and coastal surface-waters

The different types of surface-water which were recognized from the general distribution of temperature and salinity (p. 174), form, of course, a natural grouping for the T-S curves of the upper water masses. As the upwelled water has been brought to the surface from some subsurface depth offshore, its T-S characteristics are similar to those of the water at the depth from which it was upwelled, except that it has undergone a certain amount of modification in the process of uplift.

If we compare an inshore and offshore station on the first survey—stations WS 1000 and 996 (Fig. 33*a*)—it is clear that at the inshore station the upper 50 m. is composed of a mass of water corresponding to that at 200 m. at the offshore station, but warmed up, reaching a temperature of 18° C. at the surface. The low salinity (34·9‰) of this water on the surface contrasts strongly with the high salinity (35·18‰) of the oceanic surface-water. Similarly on survey II (in Fig. 33*b*) there is again a contrast, although rather less pronounced.

The T-S diagrams also demonstrate clearly the mixed nature of the water inshore at Walvis Bay on survey I. Comparing Fig. 33*c* with Fig. 33*a*, we can see that the surface-water at stations WS 979 and 980 lie somewhere between the true oceanic and true coastal characteristics.

Finally, for the 25° S. line on the first survey the T-S diagrams (Fig. 33*d*) show the 'oceanic' characteristics of the inshore 'station'.

We see, therefore, that the upwelled water originates from the South Atlantic central water, at depths of 200–300 m. Apparently the upwelled water is not subjected to any significant mixing with the warmer and more saline 'offshore' surface-waters in its process of uplift. Indeed, everything suggests that it remains quite discrete from the latter. On the sea surface, as we have already seen, there is in most cases a sharp boundary between the two types of water except in areas where mixing has obviously taken place.

It is evident that these two water masses form, on both surveys, a series of eddies along the coast, tongues of upwelled water diverging offshore and inter-locking with wedges of offshore water converging towards the coast. It is difficult to generalize about the depth to which the eddies extend, as some of them appear to retain their identity to the depth of upwelling while others are very much shallower.

Dynamic height anomalies

Owing to the lack of direct observations of surface-currents it has been necessary to resort to some indirect method of estimating the actual water movements which were taking place during the surveys. The most widely used of such methods is that based upon the theorem developed by Bjerknes

(Sandstrøm, 1919). Other methods, such as the isentropic analysis used by Montgomery (1938), have in certain cases an advantage, but after experimentation with both methods, and bearing in mind that the observations do not properly satisfy the requirements of either, a straightforward presentation of the dynamic height anomalies has been made. A few words may be said about the theoretical implications of this method in so far as the present work is concerned.

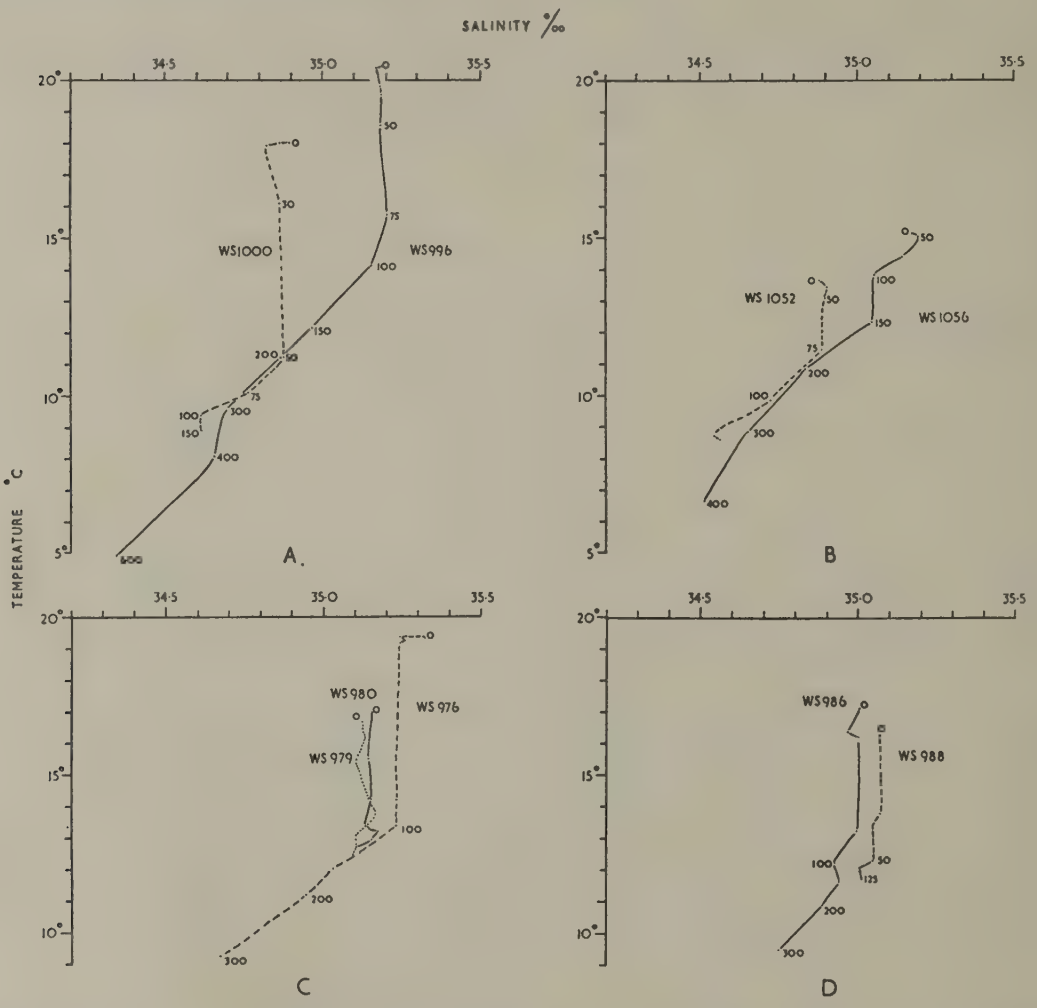

Fig. 33. Temperature–salinity relationships at 'William Scoresby' stations. (*a*) WS 996 and WS 1000 (broken line) off Orange river mouth, survey I. (*b*) WS 1052 (broken line) and WS 1056 off Orange river mouth, survey II. (*c*) WS 976 (broken line), WS 979 (dotted line) and WS 980 off Walvis Bay, survey I. (*d*) WS 986 and WS 988 (broken line) off Sylvia Hill, survey I. Positions of stations are shown in Figs. 1 and 2.

First it should be noted that Bjerknes's theorem applies to currents in which a state of 'stationary motion' is maintained. In other words, it assumes that while the current flows the distribution of mass in the water remains unaltered. This implies that no mixing, or change in properties of the water particles along their path, may take place, and that no vertical translatory movement should occur. On these assumptions the horizontal movement of the water can be related to the distribution

of mass within that water. Parr (1938*b*) has already emphasized the importance of these points in interpreting charts of dynamic height anomalies.

In the waters off South-west Africa, it is quite obvious that the requirements of Bjerknes theorem are not satisfied. Clearly the wind in this region has a considerable effect on the sea-surface, and there are undoubtedly considerable vertical movements of the water masses. It is therefore considered unwise to place too much reliance on the charts as depicting actual currents, but rather to look upon them as plans of the distribution of mass within the water above an arbitrary level surface.

In the construction of the charts it is desirable to choose a surface of no motion, above which the mass of water can be calculated. In the present observations it is impossible to be certain that such a surface does exist. Normally such a surface is chosen at a considerable depth, where the movements, if any, will be so small relative to those at the surface that they can be ignored. The 'William Scoresby's' observations lie, however, for the greater part in shallow waters, and there is little likelihood that any level will present a surface of no motion in these observations[1]. As the best compromise, however, the 600 decibar surface has been chosen, and the topographies of the sea-surface, and the 200 db. surface, are shown relative to this in the charts in Fig. 34. Many of the present observations have been made in the relatively shallow waters of the continental shelf where they cannot extend to the depth of the reference surface chosen in the deeper water offshore. Helland-Hansen (1918) proposed a method to overcome this difficulty. He suggested that the land mass in the vertical section representing the continental shelf and slope, should be replaced by a fictitious body of water which is considered to be at rest, and in which the isosteric surfaces would, therefore, be horizontal. In the adjacent water mass the isosteric surfaces would tend to become horizontal as they approach the continental slope, for, owing to friction, the velocity along the sea-bed must approach to zero. For this reason Helland-Hansen suggested that the isosteres as they approach the sea-bed should be drawn horizontal and produced horizontally through the land mass, thus furnishing arbitrary levels for the calculation of the heights of the isobaric surfaces over the land mass. In face of the difficulties this seems a fairly reasonable assumption to make, but it has no physical basis whatsoever, and it is indeed difficult to imagine the existence of such an arrangement. Groen (1948) has discussed another method which was suggested by Sverdrup, and proposed yet another, that of continuing the isosteric slopes into the land mass, but it is doubtful whether these produce a picture any more realistic than that given by Helland-Hansen's method which has been used in the following.

Although a precise picture of the currents at different levels cannot be attained, it is intended that the charts should at least serve as a check on the water-movements deduced from the distribution of temperature, salinity and other properties of the water masses. The movements shown will probably be more correct during survey I when there was less vertical movement, than during survey II.

Surface topography (Fig. 34)

On survey I the most pronounced feature of the chart shows the tendency to a movement towards the coast in the latitude of Walvis Bay (23° S.). This flow appears to bend southwards along the coast and is no doubt responsible for the mixed nature of the water inshore at Walvis Bay, and the pronounced oceanic influence at the inshore stations on the 25° S. line. In its southerly movement, it displaces away from the coast the north-westerly flow of coastal waters from the south, so that in 25° S. there is a southerly movement of mixed oceanic water inshore, and a northerly movement of coastal water offshore.

[1] Attempts to define a level of no motion using techniques such as that of Sverdrup and Flemming (1941) have given little guidance with the present observations beyond suggesting that the 600 decibar surface may be one of relatively little motion.

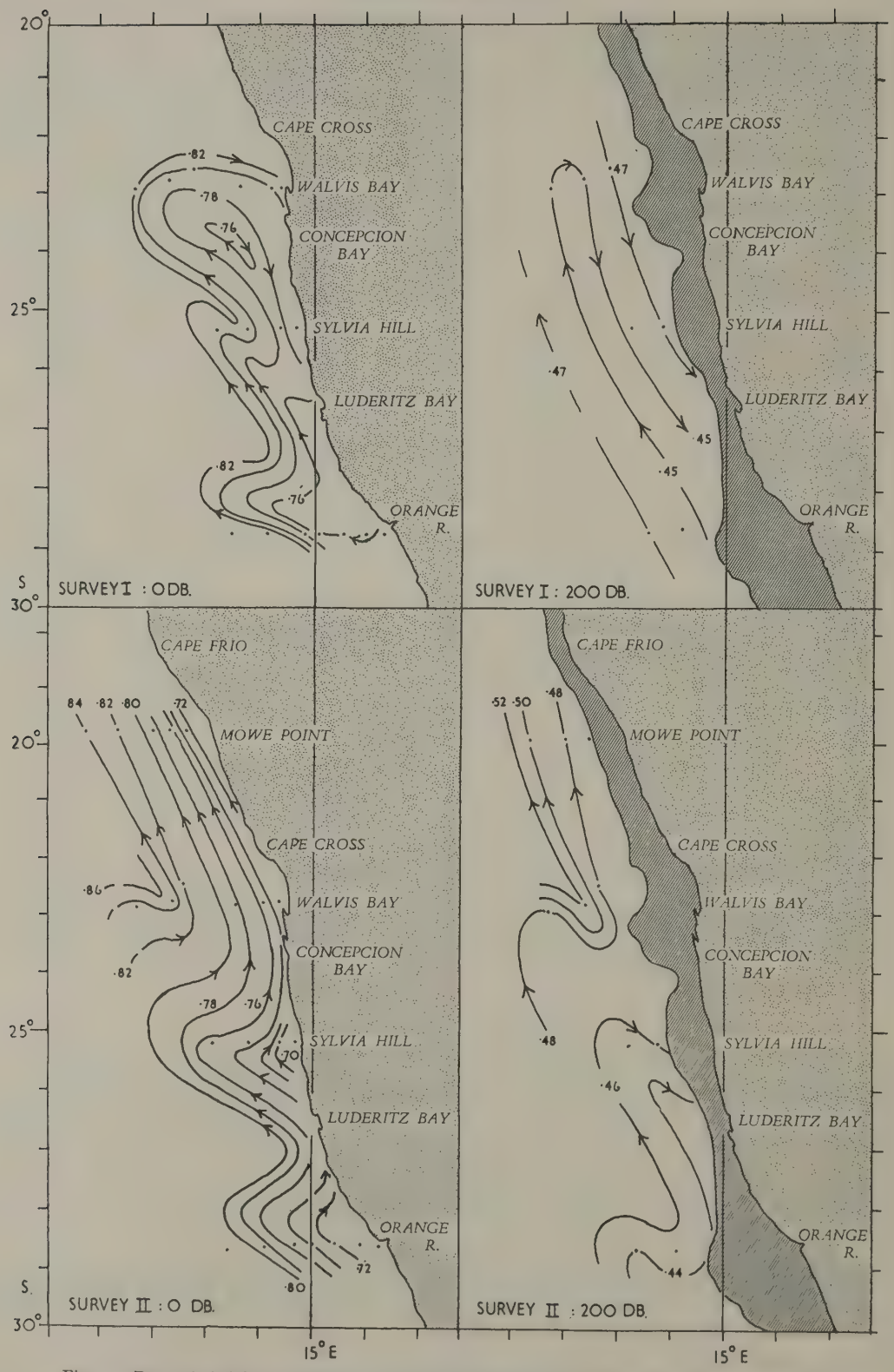

Fig. 34. Dynamic height anomalies of the sea-surface and 200 db. surfaces relative to the 600 db. surface, for survey I and survey II.

The eddy which lies to the north of the Orange river line is probably a fair representation of the westerly flow of coastal water adduced from the temperature and salinity observations.

On survey II the movements are considerably more intense. Undoubtedly the sparsity of data shows a simpler picture than is shown in the surface-temperature chart (Fig. 7*b*) which is constructed from a much greater number of observations, but within the three great eddies shown, the cooler coastal waters show a pronounced offshore, or longshore movement to the north and west. In conjunction with this the oceanic waters move in an easterly direction towards the coast.

There were very few occasions on which the set of the ship could confidently be ascribed to water-movement as distinct from wind leeway. At the station on the outer end of the Walvis Bay line on survey I a northerly set of about 1 knot was encountered with a light wind. This agrees with the computed currents (Fig. 34). The only other occasion upon which we can be reasonably certain the effect was solely due to currents was between stations WS 1057 and 1061 on survey II. When the ship was steaming north from the Orange river line stations to the inshore end of the 25° S. line, she was set 065° at ½ knot with no wind. Once more this is in agreement with the computed currents.

Topography of the 200 db. surface

The lesser number of observations at this depth give the appearance of a very simplified pattern. On survey I there is clearly a southerly movement along the coast from the north, penetrating southward and tapering in towards the coast, and finally disappearing in about 28° S. Seawards of this the water appears to move to the N.N.W.

On survey II offshore the principal movement is once more to the north, but there is some indication of a south-easterly flow on the landward side of a trough line running north-west through WS 1070. This tendency to a southerly or onshore movement at this depth in the water adjacent to the continental shelf will later (p 190.) be seen to be connected with the process of upwelling. It is postulated that this is a compensatory movement replacing the water which has been drawn up to the surface inshore and we have, therefore, called it the compensation current.[1] This southerly current is warmer and more saline than the waters seaward of it in the trough which separates it from the northerly current farther offshore.

The water masses at 200–600 m.

Generally speaking, on both surveys, the waters in this layer correspond very closely with the mean temperature-salinity relationship already outlined for the South Atlantic central water. Table 8 gives the salinity values corresponding to the given temperatures at each station. On the first survey the mean range of salinity at the given temperature is only 0·11‰, and on the second survey 0·10‰.

Table 8. *Temperature–salinity relationships of the water masses between* 200 *and* 600 m.

	Survey I						*Survey II*								
Temperature (° *C.*)	*WS 976*	*WS 977*	*WS 978*	*WS 986*	*WS 996*	*WS 997*	*WS 1102*	*WS 1100*	*WS 1098*	*WS 1080*	*WS 1081*	*WS 1079*	*WS 1070*	*WS 1056*	*WS 1055*
12·0	—	—	—	—	—	—	35·03	35·10	35·10	—	—	—	—	—	—
11·0	34·91	—	—	—	34·83	34·82	34·91	34·97	35·00	34·87	34·90	34·90	—	—	—
10·0	34·76	34·84	34·73	34·79	34·73	34·72	34·80	34·84	—	34·74	34·81	34·82	34·80	34·76	34·78
9·0	34·65	34·75	34·67	34·70	34·67	34·63	34·72	34·72	—	34·66	34·71	34·75	34·69	34·67	34·68
8·0	34·56	34·65	34·61	34·60	34·64	34·62	34·60	34·63	—	34·59	34·63	34·67	34·65	34·59	34·59
7·0	34·52	34·58	34·55	34·52	34·55	34·57	34·44	34·56	—	34·51	34·54	—	34·57	34·52	34·50
6·0	34·52	34·52	34·48	34·45	34·44	34·44	34·31	34·51	—	34·43	34·66	—	34·47	34·45	34·43
5·0	34·51	—	—	—	34·34	34·31	—	—	—	—	—	—	—	34·36	34·39

The salinity values, corresponding to the given temperatures at each station are shown in parts per thousand. Mean: Survey I=0·11‰; II=0·10‰.

[1] Yoshida and Mao (1957), and later workers have shown that divergence and consequent upwelling at the surface is likely to be accompanied by a poleward movement in the subsurface layer.

It may be said, therefore, that on the basis of the temperature–salinity relationship, it is not practicable to distinguish any significantly distinct water masses in the layer 200–600 m., and also that it is all characteristic of the South Atlantic central water. As will be shown later, however, when dealing with the non-conservative properties oxygen and phosphate, a very marked distinction is present in this layer.

The antarctic intermediate water

The depth distribution of the observed salinity minimum in this layer has already been given in Table 7. It is noteworthy that at its core off South-west Africa only 50% of the original water type is present. Later it will be shown that the upwelling takes place from considerably lesser depths than this, and it is in fact South Atlantic central water which is upwelled and not, as has often been supposed, the Antarctic intermediate water. It is true that the former may contain a little of the latter but the proportion of antarctic intermediate water must be extremely low.

UPWELLING

Previous work on the mechanism of upwelling

Several explanations have been put forward to account for the presence of the cold water along the south-west African coast. The earliest idea held was that the Benguela current was a continuation of the west wind drift, bringing down cold water from the higher latitudes of the antarctic. Ross (1847) (see p. 132), however, demonstrated that this could not be true because warmer water was present to the south of the Benguela current, cutting off any continuous flow from the antarctic. Yet this view was maintained by some authorities even as late as 1910 (Engeler). Ross did not offer any satisfactory alternative explanation to the South Polar current theory, but later workers gradually developed the idea that the cold water must come up from subsurface layers. Several suggestions were made as to how this uplift, or upwelling, came about. Witte (1880) deduced on theoretical considerations that the upwelling must be brought about either by the effect of the earth's rotation on such a meridional current as this, or possibly by offshore winds driving surface-water away from the coast. Murray (1888, 1891) showed the latter to occur in the lochs on the west coast of Scotland, where, in summertime, offshore winds produced a depression of the surface temperature along the shore. Buchanan (1880) and Buchan (1895) held that the same process was of general application to the major upwelling regions off the west coasts of the continents. Schott (1902), however, while considering that the upwelling along the north-west African coast could be explained on these grounds (as the winds blow either parallel to the coast or offshore), pointed out that this could not hold good for the south-west African coast. Here the winds were principally onshore in the coastal region.

Schott offered an alternative explanation. Since the main impulsive force of the Benguela current was the south-east trade wind, the current would be deflected, under the influence of the earth's rotation, away from the coast. The water thus removed must be replaced, and owing to the direction of the coastline this would have to be a vertical compensation. This theory Schott supported with the fact that where the African coast recedes to the north-east (in about 17° S.) the upwelling fades out and becomes an irregular phenomenon, the compensation flow then being able to take place horizontally on the sea surface from the north-east.

Thorade (1909) states, with regard to the California current, that 'Auch dieser Grund kann für uns nicht in Betracht kommen, denn einmal ist unser Auftriebgebiet bedeutend weiter von Äquatorialstrom entfernt, und dann entwickelt sich dieser [the trades] am Kräftigsten gerade während der Wintermonate, in denen die Auftrieberscheinung im Rückgange begriffen ist'. Thorade proceeded

to explain the Californian upwelling by Eckman's theory of currents. He showed that the upwelling is a direct effect of the coastal winds which on the assumptions of Eckman's theory need not blow offshore to produce an offshore transport of surface water. A wind blowing parallel to the coast would be sufficient to induce such a transport with consequent upwelling.

Sverdrup (1938), from a detailed examination of the Californian current, supports this view, and concludes that the upwelling is a direct effect of the local winds transporting surface-water away from the coast. Gunther (1936) found that on the Peru Coast the 'William Scoresby's' observations indicated that the upwelling was brought about 'as a result of wind acting in conjunction with forces due to the earth's rotation'.

The present work indicates that while the trade wind in the open ocean must maintain the denser water nearer the surface inshore, the periodic and local intense upwelling is probably mainly dependent upon the local coastal winds producing a northwards, longshore or offshore displacement of the surface water, thus initiating a vertical compensation flow from the subsurface layers.

Ekman's theory (1905) provided the basis of our present-day understanding of the effect of wind stress on the sea-surface. It shows us qualitatively that, owing to the effect of the earth's rotation and frictional forces, the drift produced by a wind blowing over the ocean deviates at an angle of 45° to the left of the wind direction in the southern hemisphere. Owing to the viscosity of the water, the velocity in this drift current will decrease regularly with depth. There will also be an increased deflection with depth, until a point is reached where the current is directed against the surface drift. At this point the velocity of the current is about 1/23rd of that at the surface, and Ekman has termed this depth (D) the 'depth of frictional influence'. While the current vectors at different levels in the wind current vary, the total transport remains directed normal to the wind direction (that is 90° to the left in the southern hemisphere).

These results apply to an ocean of which the bottom is very deep, and where the influence of coastline and varying density of the water is not considered. In this latter respect, the quantitative application of the theory is hindered, as the magnitude of the reaction between the different density layers in the sea is not known. Eddy viscosity is, however, a measure of this reaction, and more recently Rosby and Montgomery (1935) have introduced the conception of a 'mixing length' which varies with depth and upon which the eddy viscosity is dependent. On this basis they find that the deviation of the drift is not constant as Ekman postulated, but varies with the strength of wind and with the latitude. Even these improved assumptions, however, still appear to fall short of giving a realistic picture.

Ekman further studied the problem of wind drift in the presence of coastlines and where the sea bottom was shallow. Where the bottom is greater than twice the depth of frictional influence it does not have much influence, but in shallower water there is a restriction of the deflection and slowing of the turning with depth, until in very shallow water the whole movement follows the direction of the wind (the effect of the earth's rotation in this case being negligible). Thus in coastal regions three main factors affect the wind drift.

1. The position of the coastline in relation to the water in question.
2. The relation between the depth D and the sea bottom.
3. The direction of the wind stress, in relation to the direction of the coastline.

The effect of winds on the South-west African coast

We can find the approximate magnitude of D in metres from the relationship:

$$D = 7{\cdot}6\, W/\sqrt{\sin\theta},$$

where the wind stress W is expressed in m./sec., and θ is the latitude. (For wind stresses <6 m./sec.

the formula is replaced by $D = 3{\cdot}67\sqrt{w^3}/\sqrt{\sin\theta}$ (Sverdrup *et al.* 1946).) Even with force 8 winds the depth D is of the order of 200–250 m., and therefore it is evident that only in the coastal region will D have an effect upon the wind current. The region where the south-east trade prevails, outside the continental shelf, will be void of any bottom-effects.

Thus in the open ocean the south-east trade wind will produce a surface drift in a westerly direction and a total transport of water to the south-west. The lighter surface-water will therefore be transported away from the African coastal region. The presence of the coastline, however, prevents any surface replacement of this water in the coastal region, and therefore a vertical replacement or upwelling must follow. This vertical movement in the coastal region will create a distribution of density such that the heavier water lies against the coast, and a relative current will be produced running northward along the coast.

The intensity of this relative current will depend upon both the direction of wind and the direction of the coastline. Now, in South-west Africa, the coast runs N.N.W. to S.S.E. and the trade wind is south-easterly becoming more southerly in higher latitudes. The angle between the wind and the coast increases, therefore, from south to north, and one might expect from this an intensification of the relative current to the north.

The total transport of the wind current is, however, directly proportional to the wind stress and inversely proportional to the sine of the latitude, so the decreasing strength of the trade wind to the north of the region will tend to reduce the intensity of the relative current. The ultimate development of the latter will depend on the magnitude of these various effects.

The winds in the coastal region must have an additional modifying influence on the relative current set up by the trade wind. Furthermore, as we pass into the coastal region the sea bottom, rising to the continental shelf, will have an increasing effect on the deflection of the wind current from the wind stress. It is not practical, however, to calculate the deflection as the coast is approached, since the wind also veers the nearer the coast one gets.

Observed winds and hydrographical conditions

The synoptic charts of the South-west African Weather Bureau show that in September–October the trade winds were consistently stronger than in February–March. Theoretically this would have given rise to a greater relative current along the coast in the former months.

To estimate the effect of the coastal winds upon this relative current the wind vectors for three coastal stations have been plotted (Fig. 35) on the assumption that they would produce a surface drift at 45° to the left of the wind direction. All such vectors producing a drift between a line parallel to the coast to the north and a line normal to this offshore, have been considered positive, while all other winds have been taken as negative. From this figure it can be seen that during the first survey the coastal winds would only be expected to intensify the relative current off Luderitz Bay, little effect being exercised by the light winds and calms at Walvis Bay and Orange river. On the second survey in September–October there was a greater amount of coastal wind, particularly at Walvis Bay and Luderitz Bay At Luderitz, it was predominantly positive and so would have intensified the relative current, while at Walvis Bay the greater variation of direction might have been contributory to a more rapid breakdown of the relative current into eddies.

The relatively calm spells at Walvis Bay and Orange river in March are reflected in the absence of convection layers in these sections while the greater wind stress in spring is associated with better mixed inshore waters in that season (Table 5).

A comparison of these features of the wind activity with the distribution of surface temperature and salinity on the two surveys suggests that the localized intensification of upwelling and indeed the

breakdown of the relative current into eddies may be largely dependent on the localized coastal winds. Clearly, however, a correlation between such observations as wind observed at coastal stations, within some modifying influence of the land, and hydrographical observations at sea must at best be rather rough, and a more satisfactory correlation might be expected if it were possible to compare the winds at sea with the coincident hydrographical changes. The only opportunity which we have of making

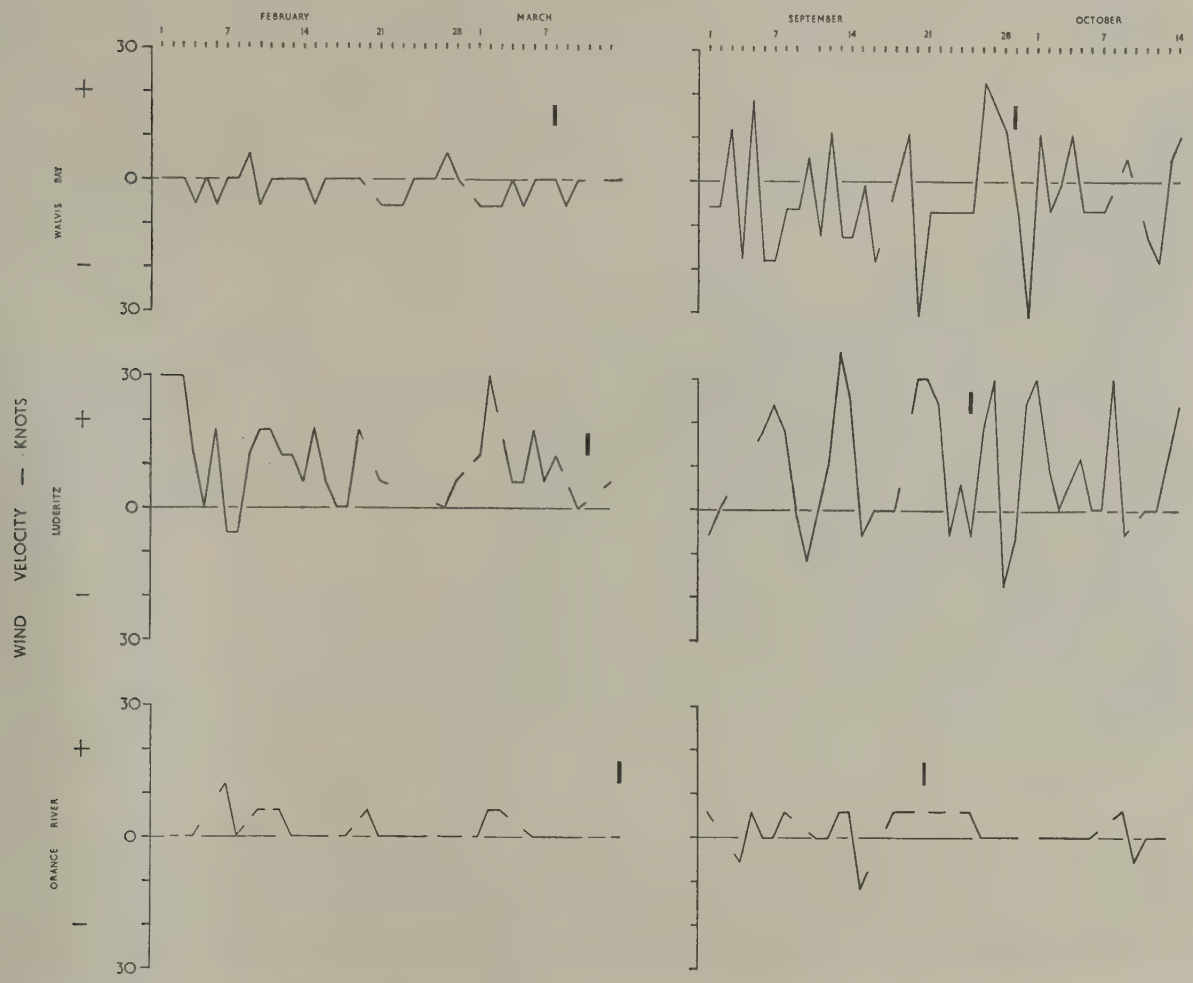

Fig. 35. Predominant coastal wind vectors before and during the two 'William Scoresby' surveys at three points on the coast—Walvis Bay, Luderitz Bay and Orange river mouth. Winds which would produce a longshore northwards, or offshore drag on the sea-surface are taken as positive and other winds as negative. Wind speeds are in knots. Heavy black lines indicate the beginning of the survey in each position.

such an estimate of the short-term effect of the wind on the sea-surface was the occasion of a S.S.E. gale off Walvis Bay. While steaming west along the Walvis Bay line on the second survey the ship was forced to heave-to for nearly 48 hr. When the gale subsided the ship returned eastwards, and a comparison of the sea-surface temperatures before and after the gale reveals some interesting features.

In Fig. 36 the sea-surface isotherms have been drawn from the station observations and the distant-reading thermograph records; they are in black for the westward passage preceding the gale, and in red for the eastward passage following the gale.

During the period of this gale the wind records at Walvis Bay do not show any particularly stormy trend, and so it appears, as indeed one might expect, that the gale was solely due to increased velocity of the trade wind.

In interpreting the results certain assumptions must be made. First, surface heating must be assumed to have been regular within the region in question. Secondly, the turbulent mixing of the upper water layers must be assumed not to have had any great effect in the lowering of temperature in the surface waters. This latter seems justifiable since the depth of the mixed layer at WS 1079 before the gale was 50 m., and within this the temperature was nearly uniform.

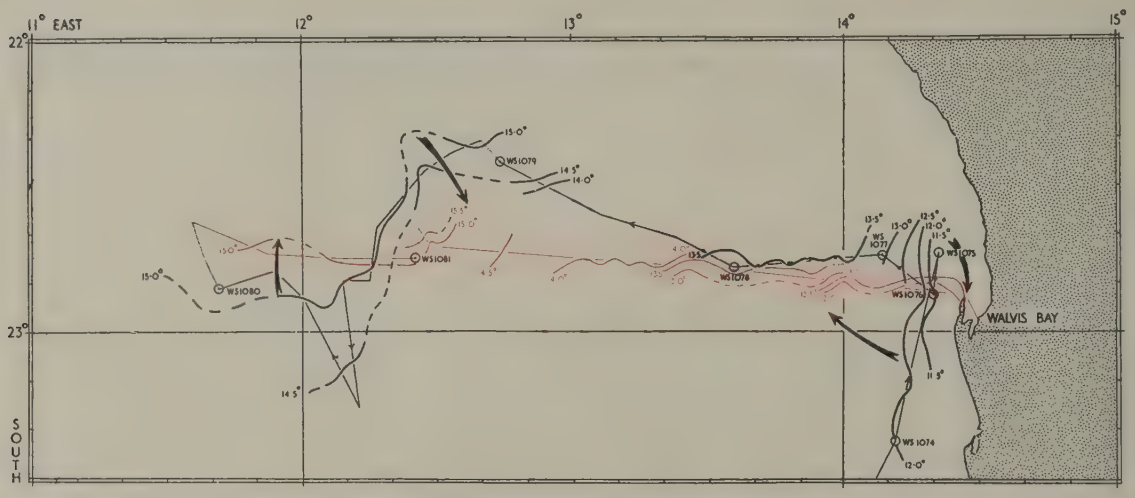

Fig. 36. Effect of wind and surface-temperature. The ship's track, stations and isotherms are shown in black for the westward passage along the line of stations off Walvis Bay. While at the seaward end of this line, a S.S.E. gale was encountered which blew for about 24 hr. at Beaufort force 8–9. Subsequently the ship returned eastward to Walvis Bay, completing WS 1081 *en route*, and the track and isotherms on the return journey are shown in red. Probable surface water-movements during the interval are indicated by the arrows.

If these assumptions are correct we can imagine that the clockwise rotation of the isotherms offshore was indeed the result of a clockwise water-movement. The change inshore suggests that an offshore movement south of the line had been accompanied by a landward compensation flow in two wedges, one moving south through the position of WS 1081, and the second right inshore at Walvis Bay.

The mechanism of upwelling

With the accumulation of further theoretical knowledge of the movements of ocean currents it was soon to be realized that upwelling was probably a far more complex process than a simple uniform uplift of the subsurface layers. Without any factual data at his disposal, Bobzin (1922), in the third part of his work, viewed the movements of the Benguela current from a theoretical angle. His deductions, based on a consideration of the general principles of the movements of ocean currents, suggested that the Benguela current existed in the form of a left-handed screw, proceeding towards the equator. This conclusion, in view of later work, seems to have been almost a premonition.

Gunther (1936) found from the 'William Scoresby' observations in the Peru current that the upwelling was a localized phenomenon, and took place within a series of well-defined horizontal eddies, while Defant (1936) working on the 'Meteor' data from the South-west African region developed

a schematic system for the upwelling there, although his data were too widely scattered to obtain as detailed a horizontal picture as Gunther did.

Defant started by considering theoretically what events would occur in a long straight canal over which a wind was blowing. If two bodies of water of different density are superimposed in the canal, and if the canal runs north and south in the southern hemisphere and has a wind blowing over it from

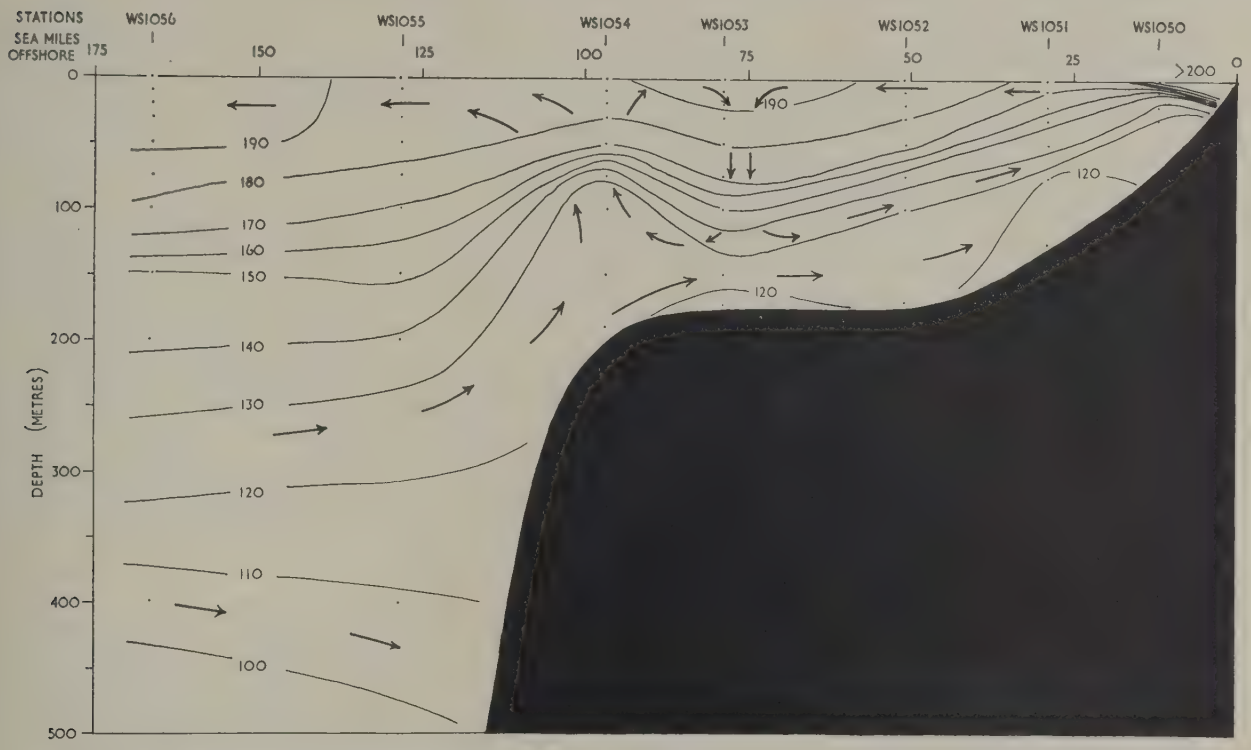

Fig. 37. Distribution of the anomaly of specific volume. Section off the mouth of Orange river on survey II. The probable direction of water-movement in a vertical plane, deduced from the shape of the isosteres, is also indicated. Positions of stations are shown in Fig. 2.

south to north, then the upper water layer would be set in motion. Under the provisions of Ekman's theory of wind drift, and when the thickness of the upper water layer is greater than the depth of frictional resistance, the lower water layer should remain at rest, while the boundary between the two would take up a slope across the canal. This slope would rise to the right (east, if one faces in the direction of flow of the surface-current) and thus the underlying heavier water would accumulate on the right-hand side of the current. At the same time a transverse circulation would form in the upper layer, which would depend on the velocity and direction of the wind. The upper layer circulation will form a left-handed screw motion. This would be strongest if the wind blew from the east, and suppressed if it blew from the west.

Applying these deductions to the South-west African coast we can regard the coast as the canal bank on the east. The west bank is missing, but this does not matter since the wind which is being applied (the south-east trade) is of limited lateral extent. Defant thus deduced a circulation pattern as in his fig. 7. The circulation is complicated by the fact that in the sea there are not two separate well-defined density layers but a general increase of density with depth. The trade wind induces a transverse circulation similar to that in the canal, a horizontal axis being present above which the water

moves to the west, while below the water rises to the east. The trade wind, however, does not extend right into the coast, and so inside its coastal boundary the surface-water is not drifted to the west, but moves north purely by virtue of the distribution of density. This agrees with the conception of a one-sided divergence which Defant derived from the surface-current pattern and showed in his fig. 7.

Sverdrup (1938) was more fortunate than Defant in having at his disposal detailed repeated observations off the coast of California. From these he was able to calculate directly a vertical velocity-profile across the upwelling region, and to relate it to the prevailing wind vectors as recorded at coastal stations during the surveys. From this, Sverdrup argues that as upwelling occurs along the coast, the dense upwelled water is in time transported offshore as was the surface-water which it arose to replace. Eventually conditions will be set up whereby a convection cell develops between the denser water lying on the surface and the lighter offshore water, this cell becoming sharply enough defined to be regarded as a boundary.

That such a mechanism operates on the South-west African coast we cannot be certain, but the available evidence strongly suggests that it does. The pattern of the isosteres on the Orange river line (survey II, Fig. 37), which is probably the most complete section through an area of active upwelling, is the best guide to an interpretation of such movements. Assuming the surface-waters to be under the stress of a wind effective in their offshore transport, the distribution of mass on this section can be interpreted on the basis of the water-movements suggested by the arrows. The convection cell between stations WS 1053 and 1054 marks the boundary between the coastal and oceanic water types, to which reference has already been made, and seems to act like a roller bearing between the two systems of water-movement. Movement of this boundary to the west (left) would be accompanied by an upwelling from about 300 m. depth.

Depths affected by upwelling

The most straightforward method of determining the depth of upwelling is to utilize the T-S diagrams. From these it is possible to determine from what depth in the offshore water the coastal waters originate. On p. 179 it was shown that in the process of uplift from subsurface depths, the coastal waters remained discrete and that a rise in their temperature was the only important change that took place. If then we take the origin of the T-S curve for the coastal waters at the point where it arises from the T-S curve of the offshore water, the depth on the offshore T-S curve will give us a measure of the depth of origin of the coastal water. These depths are set out in Table 9. The first figure shows the depth from which water is elevated to the surface. Where a range of depths are shown the second figure represents the maximum depth affected, but it is not necessarily implied that water is brought from this depth right to the surface. It is normally elevated from this depth to a somewhat lesser depth on the continental shelf.

Table 9. *Depth of upwelling*

Latitude	*Survey I* (*m.*)	*Survey II* (*m.*)
19° 44′ S.	—	220
23° S.	—	200–230
25° S.	*ca.* 200	275–300
28° 30′ S.	200–350	180–320

Centres of upwelling

The recurrence of upwelling in particular localities has been demonstrated by Schott (1931) and Gunther (1936) in the Peru current. In the Benguela current this question has not received so much attention, but Copenhagen (1953) has suggested that seven such localities exist off the South-west African coast. He goes on to correlate these centres with the bottom topography. The position of the centres of upwelling is deduced from a comparison of the coastal temperature with the temperature of an arbitrary latitudinal standard, taken by Copenhagen as the temperature 200 miles from the coast.

Although the 'William Scoresby's' observations are insufficient to apply this method, it is noteworthy that the areas of low surface-temperature (Fig. 7*a*, *b*) were found in more or less the same regions as those outlined by Copenhagen, that is to say: (1) Saldanha Bay to Orange river mouth; (2) north and south of Luderitz Bay and extending to Walvis Bay on survey II; (3) Cape Frio to Cunene river mouth.

A closer examination of the charts, however, shows that the colder water in the vicinity of Orange river mouth lay in 28° S. in survey I, while in survey II it was centred on 29° S. some 60 miles farther south. It is noteworthy also that the 200 m. contour representing the edge of the continental shelf is 50 miles offshore in 28° S., but 90 miles offshore in 29° S. This area of cold water appeared to show no particular correlation with the topography of the sea-bed.

Probably the most that can be said from the present results is that the conditions on survey II, which represent a characteristically active period of upwelling, show that upwelling was most pronounced in the regions: (1) from 29° to 30° or 31° S.; (2) from 28° S. to Luderitz Bay and northwards to Walvis Bay; (3) possibly an additional area from Cape Frio to Cunene river mouth. To the south of 30° S. we have insufficient data to allow any conclusions to be drawn.

Influence of the direction of the coastline

The absence of any pronounced upwelling from Cape Frio southwards to 22° S. while it is present both to the north and south of this area appears to be rather significant when the shape or direction of the coastline is considered. North of Cape Frio, the coastline runs approximately north–south. From Cape Frio to Walvis Bay its direction changes to about 330° to 150° and south of Walvis Bay to about 352° to 174°. With a S.S.W. (202½°) wind, assuming that the drift is 45° to the left of the wind direction, the resultant water-movement in the region between Cape Frio and Walvis Bay would be in the direction 160° to 340° about 10° onshore towards the coast. Clearly, therefore, along this stretch of coastline the effect of the sea-breeze which is S.S.W. in this area would be to pile water against the coast, rather than remove it and create upwelling.

North of Cunene river mouth (17° S.) the coastline bends away gradually in an easterly direction. This marks the northern boundary of the upwelling and it is possible that Schott's suggestion that the replacement flow for water carried offshore by the wind can occur on the surface, without necessitating the vertical circulation of upwelling along this stretch of coast.

The southern boundary of the current which lies at the Cape of Good Hope may also be considered to be an effect of the direction of coastline relative to the wind direction.

Seasonal variation of upwelling

The observations made by the 'Willlam Scoresby' cannot alone be regarded as illustrative of seasonal variation of the current. The overall lower temperatures and greater wind and upwelling during survey II, while probably characteristic enough of winter conditions, could no doubt be found at least to some extent at almost any time of the year in suitable meteorological conditions. It is, therefore,

more desirable to look upon the difference between the two surveys as an example of the current in two phases—at survey I a quiescent phase subsequent to upwelling, and at survey II a phase of active upwelling.

It is very difficult to determine how much the upwelling varies throughout the year. Clearly it is a phenomenon which can occur at all seasons. Schott (1902), Franz (1920) and Bobzin (1922) have all endeavoured to make estimates of the intensity of upwelling at different seasons.

Schott based his estimate on the extent of the upwelling zone and a comparison of the temperature of the inshore waters with that of the offshore waters at a distance of about 300 km. from the coast, and he agrees with Franz in placing the maximum period of upwelling in August and the minimum in summer. Schott, however, put the minimum in November and Franz in February. Bobzin, on the other hand, derived his estimate from a comparison of the mean monthly and mean yearly temperatures and their mean variation, and this led him to conclude that upwelling reached its maximum in summer (October–December) and its minimum in June.

Bobzin ascribed the discrepancy between his results and those of Schott and Franz to the effect of solar heating of the upwelled water, which would be at its greatest in summer and at its minimum in winter, thereby masking the true changes of temperature due to upwelling. The criteria used by Bobzin to estimate the upwelling are based on somewhat abstract considerations. Moreover, his conclusions are based on a large number of temperature observations taken at Swakopmund and Luderitz Bay—only two points on a coastline some 1000 miles in length. It seems doubtful, therefore, whether Bobzin's 'Relatives Mass des Auftreibbewegung' produces any more accurate a picture than derived by Schott and Franz.

On the assumption that wind is the primary cause of upwelling, then we may consider the winds to be as good a measure as anything else of the frequency of upwelling. In winter the trade winds are slightly stronger than in summer, and one might expect a consequent intensification of the relative current in winter. On the other hand, it is evident from Fig. 5 that the coastal winds reach their greatest upwelling effect in that season. Clearly the crucial point is the relative effect of the trade wind and the coastal wind, but without more detailed observations we can go no further.

NON-CONSERVATIVE PROPERTIES

The distribution of dissolved oxygen

Since dissolved oxygen is related to the biological process in the sea, its distribution is governed not only by water-movements and interchange with the atmosphere, but also by the varying biological activity in the water masses.

The oxygen content (Figs. 38–44) usually reaches its maximum concentration in the surface-layers of the sea as a result of atmospheric exchange and the photosynthesis of the phytoplankton in these layers. Beneath the surface-layers the oxygen content decreases towards the sea-bed. Normally in sea-waters the oxygen content remains fairly high in the deeper layers, but off South-west Africa there is a very rapid decrease with depth in the inshore waters, so that even in normal conditions in this region a content of less than 1 ml. O_2/l. is found in the vicinity of the sea-bed on the continental shelf. The sections from survey II (Figs. 41–4) show that the layer of low oxygen slopes upwards towards the surface as the coast is approached. Furthermore, it extends beyond the edge of the continental shelf, producing a layer of minimal oxygen content adjacent to the continental slope, at depths of about 400 m. on survey II.

On survey I this layer of minimal oxygen is much more pronounced, not only offshore, but also inshore where it extends to the sea-surface at the coastal station WS 981 off Walvis Bay (Fig. 40).

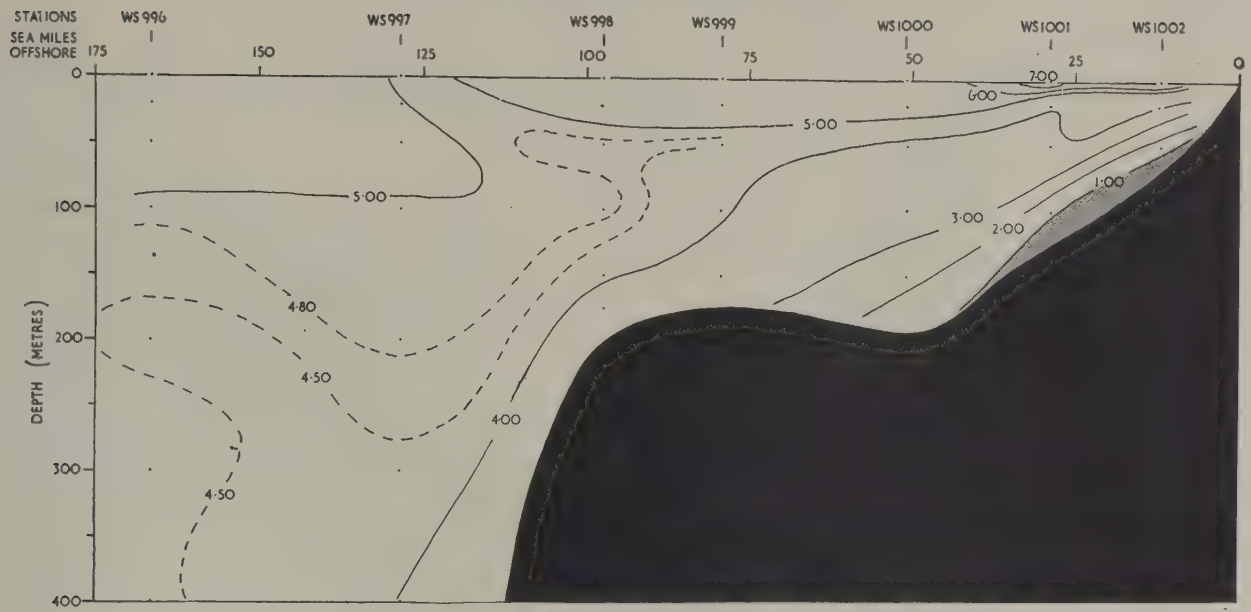

Fig. 38. Distribution of dissolved oxygen. Section off the mouth of Orange river, 12–14 March 1950, survey I. Positions of stations are shown in Fig. 1.

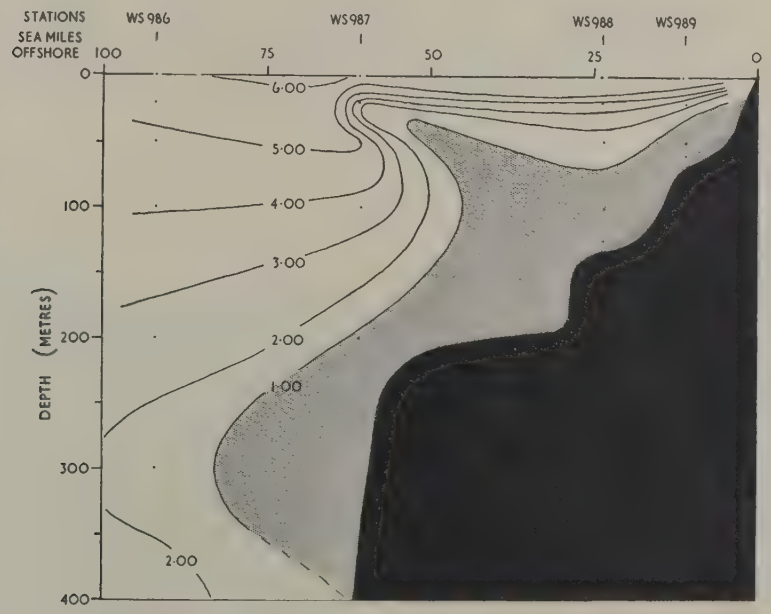

Fig. 39. Distribution of dissolved oxygen. Section off Sylvia Hill, 10–11 March 1950, survey I. Positions of stations are shown in Fig. 1.

Here, even with a recorded phytoplankton population of more than 10^7 cells (Table 14) the surface-water was only 5·8% saturated with oxygen (cf. Steeman-Nielsen, 1957, p. 75).

A comparison of the oxygen sections with those of temperature and salinity shows that the low oxygen content exhibits features of distribution similar to those of the upwelling water. Therefore

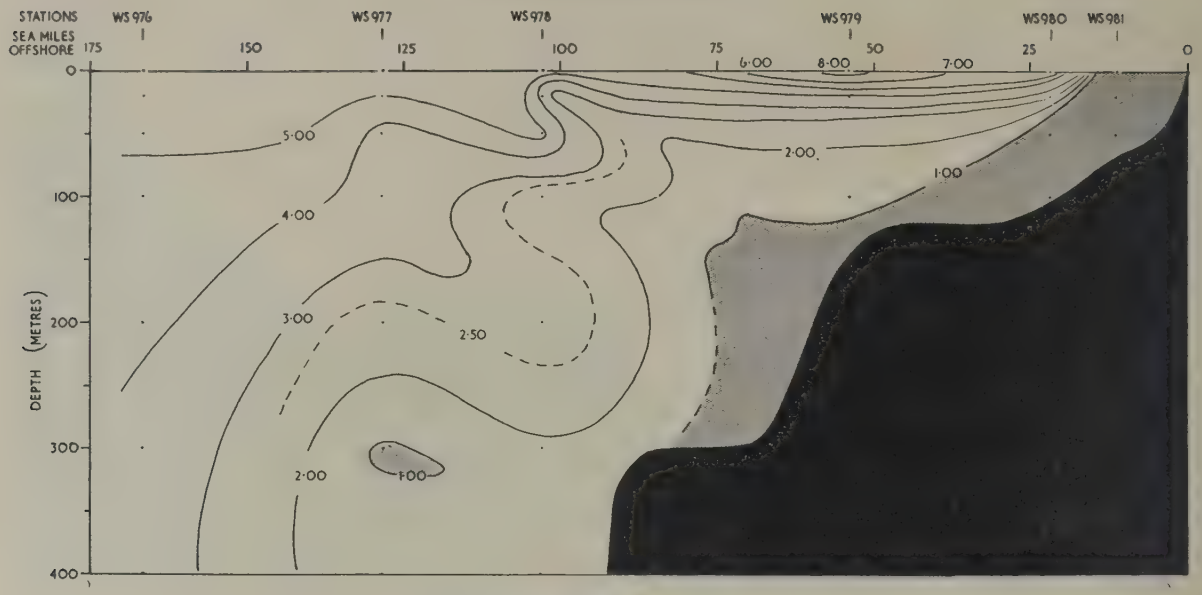

Fig. 40. Distribution of dissolved oxygen. Section off Walvis Bay, 6–8 March 1950, survey I. Positions of stations are shown in Fig. 1.

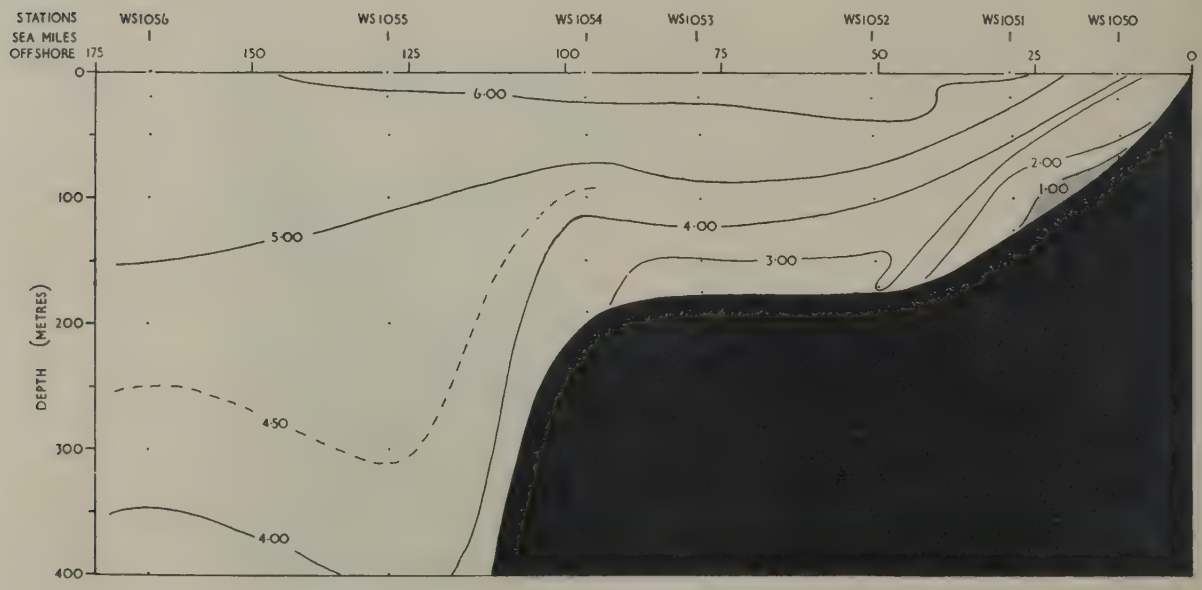

Fig. 41. Distribution of dissolved oxygen. Section off the mouth of Orange river, 21–24 September 1950, survey II. Positions of stations are shown in Fig. 2.

to trace its origins let us first examine the waters at subsurface depths adjacent to the continental shelf, from which the upwelling occurs.

If we plot the dissolved oxygen content against temperature for survey I in the 200–600-m. layers (Fig. 45), we see that the stations closer to the continental shelf and to the north of the region have the lowest oxygen content, while those farther offshore and in the south have a higher oxygen content.

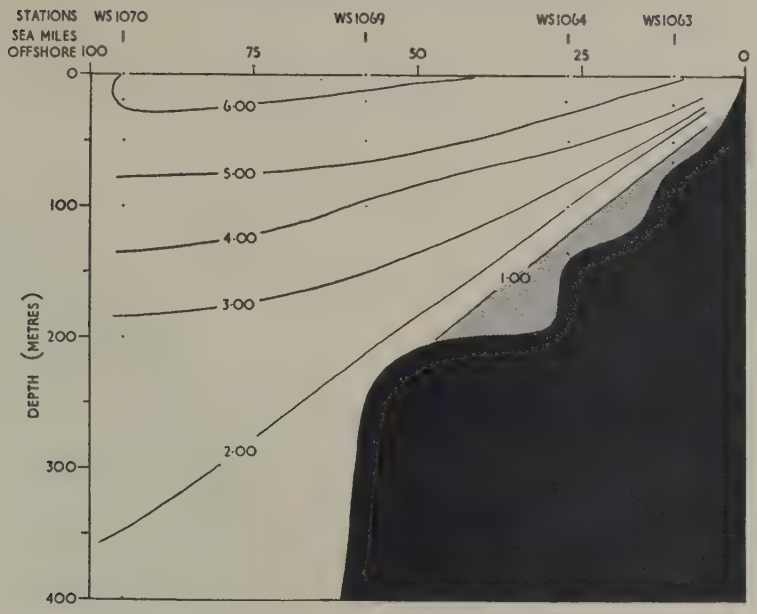

Fig. 42. Distribution of dissolved oxygen. Section off Sylvia Hill, 25-27 September 1950, survey II. Positions of stations are shown in Fig. 2.

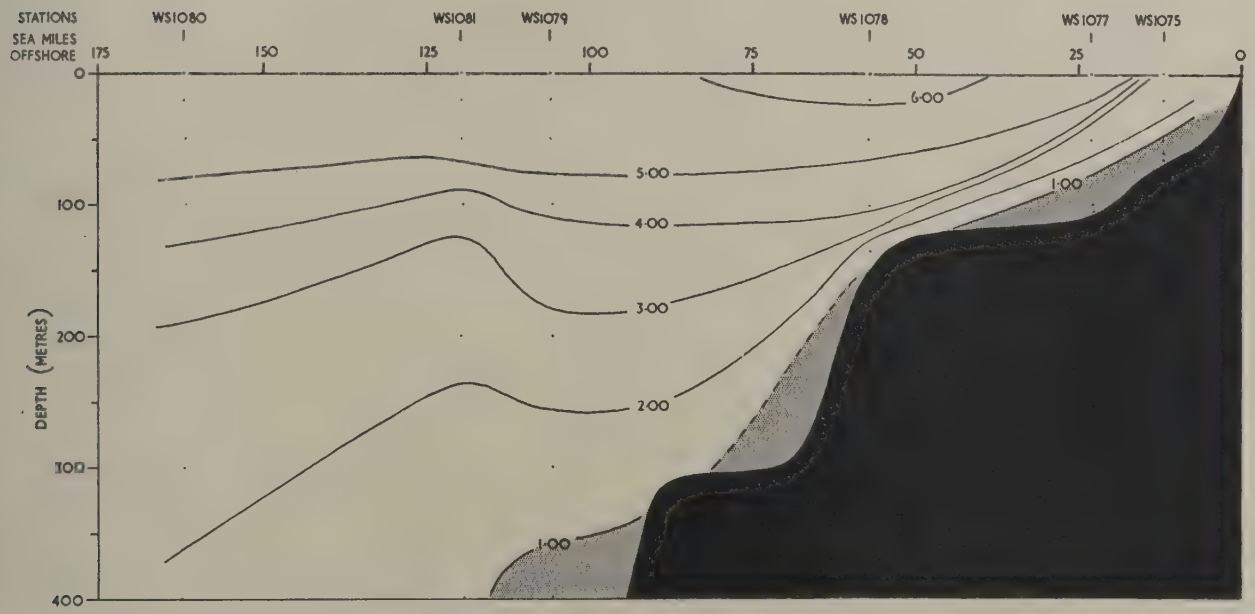

Fig. 43. Distribution of dissolved oxygen. Section off Walvis Bay, 29 September–3 October 1950, survey II. Positions of stations are shown in Fig. 2.

It was suggested on p. 183 that the water against the edge of the continental shelf at these depths exhibited a southerly movement, and therefore it is interesting to amplify our own results from some stations of the 'Meteor' (Wattenberg, 1933) to the north and south of the region. These are plotted in Fig. 46 and show a still wider contrast between the stations in the north and in the south. The positions of the 'Meteor' stations are shown in Table 10. The two curves from the 'Meteor' stations

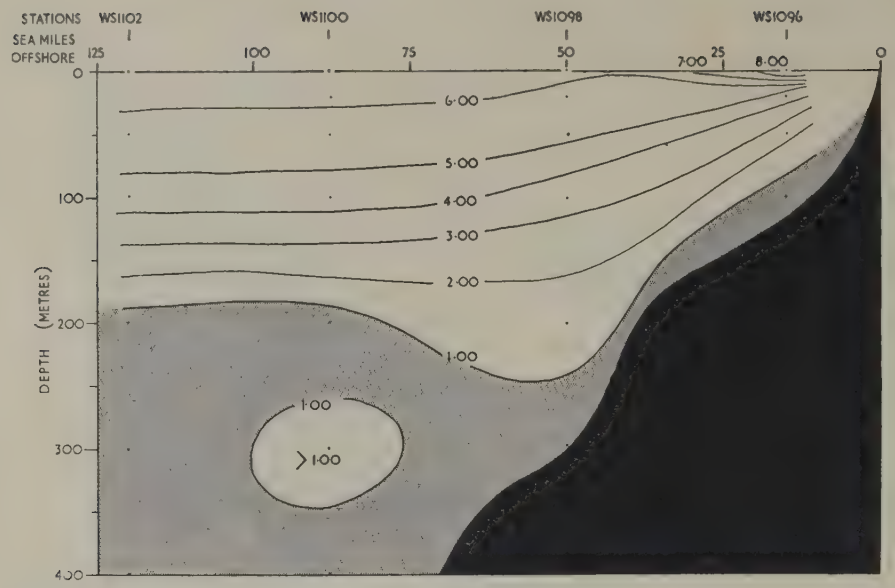

Fig. 44. Distribution of dissolved oxygen. Section off Möwe Point, 9–11 October 1950, survey II. Positions of stations are shown in Fig. 2.

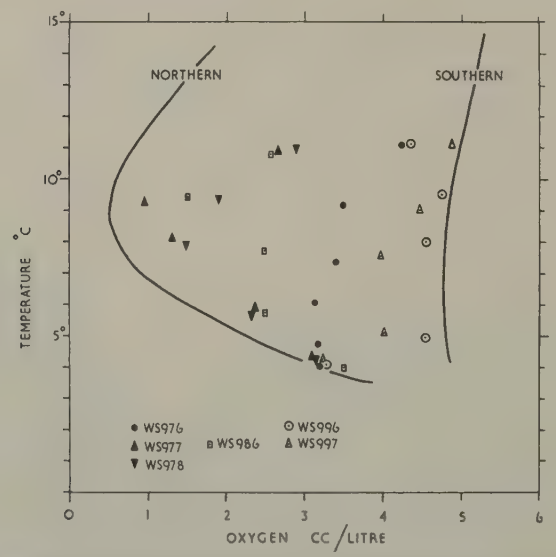

Fig. 45. Temperature and oxygen in the 200–600 m. layer at the 'William Scoresby' stations, survey I. Positions of the stations are shown in Fig. 1. The two heavy lines are taken from Fig. 46, and show the temperature/oxygen relationships in this layer to the north and south of the area surveyed, compiled from selected 'Meteor' stations.

are reproduced in Fig. 45 and show that the 'William Scoresby's' observations lie in between these two curves, the stations in the north and closer to the continental shelf lying near to the curve for the 'Meteor's' northern stations.

The decrease in oxygen content at the northerly 'Meteor' stations between 8° and 12° C. represents the layer of minimal oxygen content which extends across the tropical South Atlantic ocean (Fig. 47). This layer Riley (1951) has shown to result probably from the balance between the rates of decomposi-

tion of detrital organic matter falling from the shallower layers, and the rate of renewal of oxygen by turbulent processes.

If, therefore, the indication of southerly movement along the edge of the continental shelf at these depths is real, such a movement would carry this oxygen-depleted layer into the region of the Benguela current in this depth horizon. The water bounding such a current to the west as shown by the offshore stations has a higher oxygen content which can be ascribed to water of the type shown by the 'Meteor' southern stations.

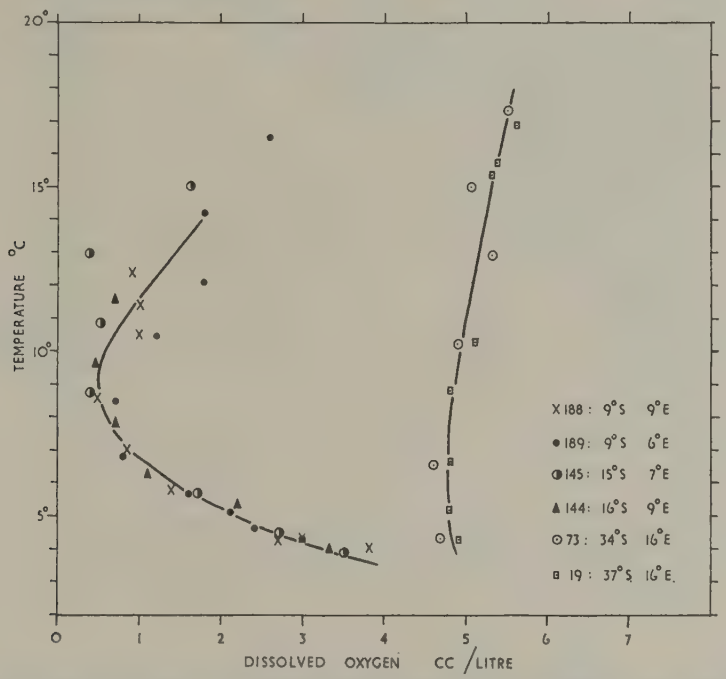

Fig. 46. Temperature and oxygen in the layer of minimum oxygen at selected stations of the 'Meteor' expedition, to the north and south of the area surveyed by the 'William Scoresby'. The positions and dates of these stations are given in Table 10.

With subsequent upwelling it might be expected that the water uplifted to the surface would be heavily depleted in dissolved oxygen and this the more so the farther north in the region. The presence of this water on the continental shelf would accentuate the effects of local decomposition of organic matter on the sea-bed, and consequently the depletion of oxygen would become more accentuated towards the coast on the continental shelf. This proceeds to such an extent that anaerobic conditions are created on the sea-bed (p. 204).

Table 10. *Positions of the Deutsche Atlantische Expedition 'Meteor' stations used in the construction of Fig.* 46

Station no.	*Position*	*Date*
19	36° 40′ S., 16° 22·5′ E.	11. vii. 1925
73	34° 02′ S., 15° 48′ E.	12. xi. 1925
144	16° 03·5′ S., 09° 29′ E.	4–5. v. 1926
145	15° 16·5′ S., 06° 32·6′ E.	6. v. 1926
188	08° 58′ S., 08° 57·7′ E.	5. ix. 1926
189	09° 00′ S., 06° 00′ E.	6. ix. 1926

Fig. 47. The distribution of the layer of minimum oxygen in the South Atlantic Ocean. From Wiss. Ergebn. dtsch. Atlant. Exped. 'Meteor', Bd. IX, Beil. XXXVII. This figure shows the oxygen content at a depth of 300 m.

Normal and abnormal conditions within the current

A comparison of the dissolved oxygen sections for survey I and survey II (Figs. 38–40 and 41–4) shows that the oxygen depletion on the continental shelf was much more pronounced during survey I, and in particular in the Walvis Bay region where even at the sea-surface inshore (WS 981) the oxygen content was only 0·33 c.c. O_2/l. The consequences of such an immense depletion of dissolved oxygen are discussed later (p. 199) in the consideration of its effects upon fish mortality, but for the present we must consider what conditions lead up to such a catastrophic event.

The maintenance of aerobic conditions on the continental shelf must be dependent to a great extent upon the renewal of oxygen by turbulent processes. In this case one would expect, as indeed is shown by the results of survey II, that in the conditions which set up a strong northerly current the introduction of more highly oxygenated water would be at its maximum, and the oxygen on the continental shelf would probably be continually renewed.

But if the currents were slowed down, stopped or even reversed, then the converse might be expected to occur. The turbulent renewal of oxygen would be at its minimum, the effects of decomposition on

the anaerobic sea-bed would become magnified, and the production of hydrogen sulphide by the sulphate-reducing bacteria in the bottom sediments (p. 204) would assist in the depletion of oxygen.

The conditions found at Walvis Bay on survey I exemplify this. The previously upwelled waters, warmed and mixed with the influx of oceanic water, may be considered to have produced almost stagnant conditions in this region, and some few days before our arrival in Walvis Bay a small mortality of fish was observed by the local inhabitants.

The meteorological records (Fig. 35 and Table 3) show that, prior to our arrival in Walvis Bay, there had been a predominance of calm and northerly winds for at least four or five weeks. It is highly probable that adverse weather conditions such as these must be responsible for the occurrence of such conditions of stagnation as are eventually associated with fish mortality.

These abnormal conditions always occur in the summer (Copenhagen, 1953) during which time northerly winds predominate at Walvis Bay. This fact is not shown to advantage in Fig. 5, probably

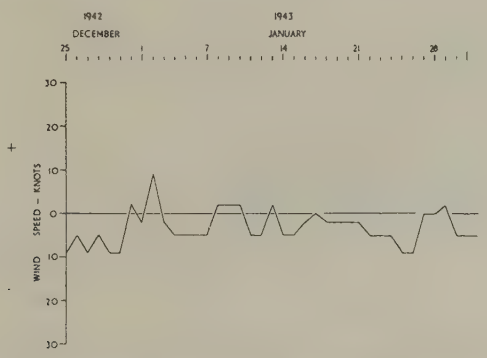

Fig. 48. Predominant wind vectors at Walvis Bay during the fish mortality of the summer of 1942/3. The wind vectors are plotted in the same manner as in Fig. 35. From the records of the climatological station at Walvis Bay.

because these winds represent rather exceptional circumstances, and they do not necessarily occur in every year. Other opportunities do occur, however, of comparing these abnormal conditions with meteorological records.

In January of 1943 a considerable mortality of fish was reported by Dr McConnel at Walvis Bay (Brongersma–Sanders, 1948). It extended from Walvis Bay to Concepcion Bay, a distance of some 60 miles along the coast.

At this time hourly meteorological observations were taken at Walvis Bay. The winds recorded there are plotted (Fig. 48) in the same manner as in Fig. 35, any winds between south-west through south to east-south-east being counted as positive and all other winds as negative. The negative winds, mainly north to north-west, are those which would have been conducive to the abnormal conditions, and Fig. 48 shows that they persisted throughout January 1943.

A mortality of much greater extent occurred in the summer of 1924–5 (Reuning, 1925) and the wind records from Walvis Bay (Fig. 49) again show that after the end of December conditions would have been favourable for the production of abnormal conditions.

One further example is a smaller mortality observed at Walvis Bay in December 1925, and throughout this month the winds were either northerly or calms.

There appears, therefore, to be a well-defined correlation, at least between the occurrence of fish mortalities and the spells of calm weather or northerly winds, which create abnormal conditions in the vicinity of Walvis Bay.

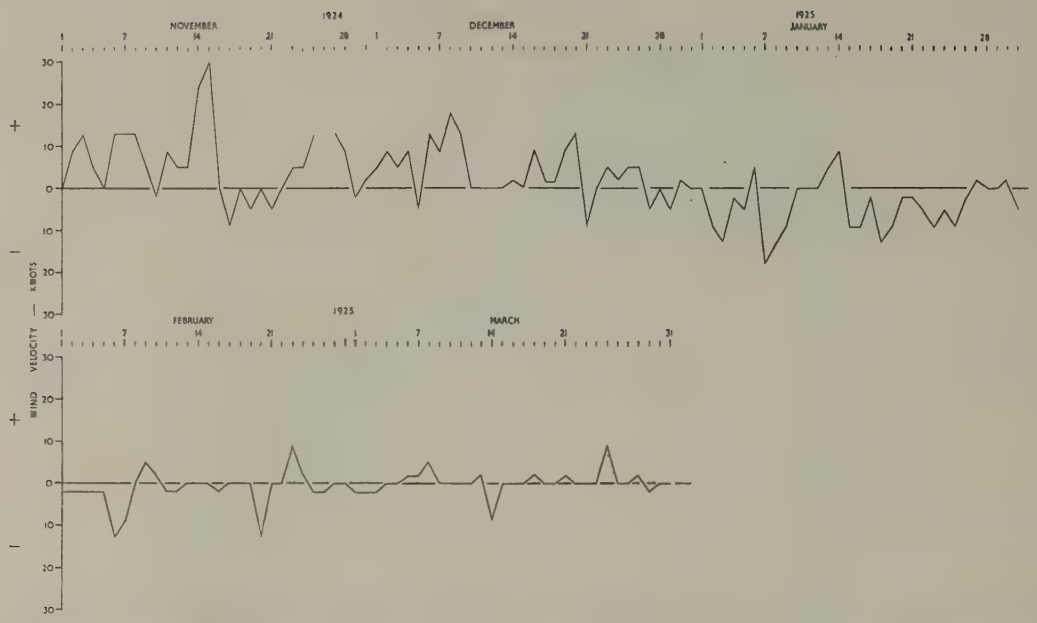

Fig. 49. Wind vectors at Walvis Bay preceding and during the fish mortality in the summer of 1924/5. The wind vectors are plotted in the same manner as in Figs. 35 and 48. From the records of the climatological station at Walvis Bay.

Fig. 50. Distributions of phosphate (mg. ats. P/m.^{3}). Section off the mouth of Orange river, 12–14 March 1950, survey I. Positions of stations are shown in Fig. 1.

The distribution of dissolved inorganic phosphate-phosphorus

The sections showing the distribution of inorganic phosphate (Figs. 50–6) indicate that on both surveys the pattern of distribution is essentially similar.

The lowest phosphate concentrations are found in the oceanic surface-waters, where from a com-

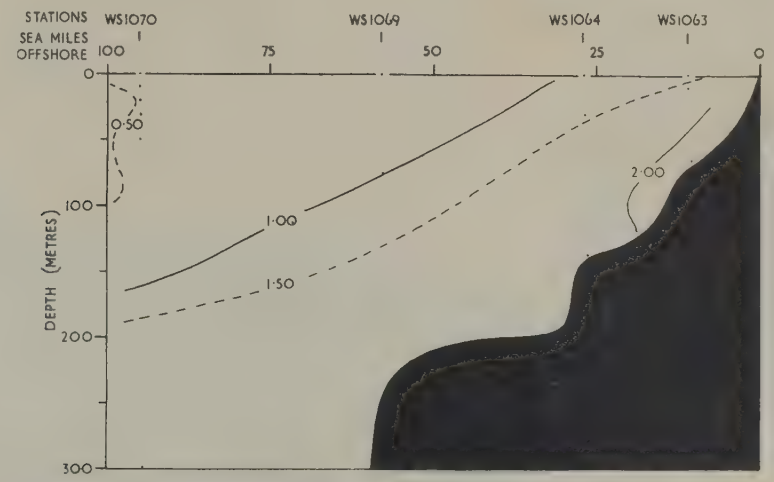

Fig. 51. Distribution of phosphate (mg. ats. P/m.³). Section off Sylvia Hill, 10–11 March 1950, survey I. Positions of stations are shown in Fig. 1.

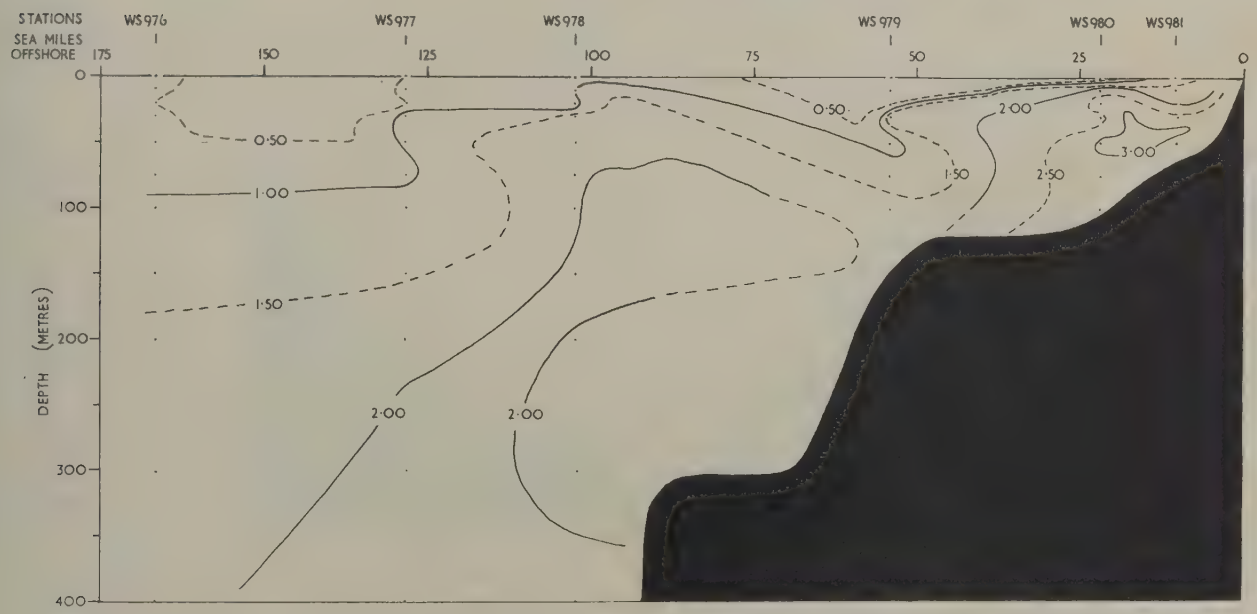

Fig. 52. Distribution of phosphate (mg. ats. P/m.³). Section off Walvis Bay, 6–8 March 1950, survey I. Positions of stations are shown in Fig. 1.

plete absence of phosphate values of up to 0·5 mg. ats. P/m.³ were found. The upwelled coastal waters present a sharp contrast. In them the phosphate content is very high, on occasion reaching more than 2·0 mg. ats. P/m.³.

Below the surface-waters the phosphate concentration increases down to the sea-bed inshore and

to greater depths offshore. In places there is a layer of maximal phosphate off the edge of the continental shelf. This coincides approximately in depth with the layer of minimal oxygen, but like the maximal phosphate layer in the equatorial parts of the ocean, it is much less well defined than the

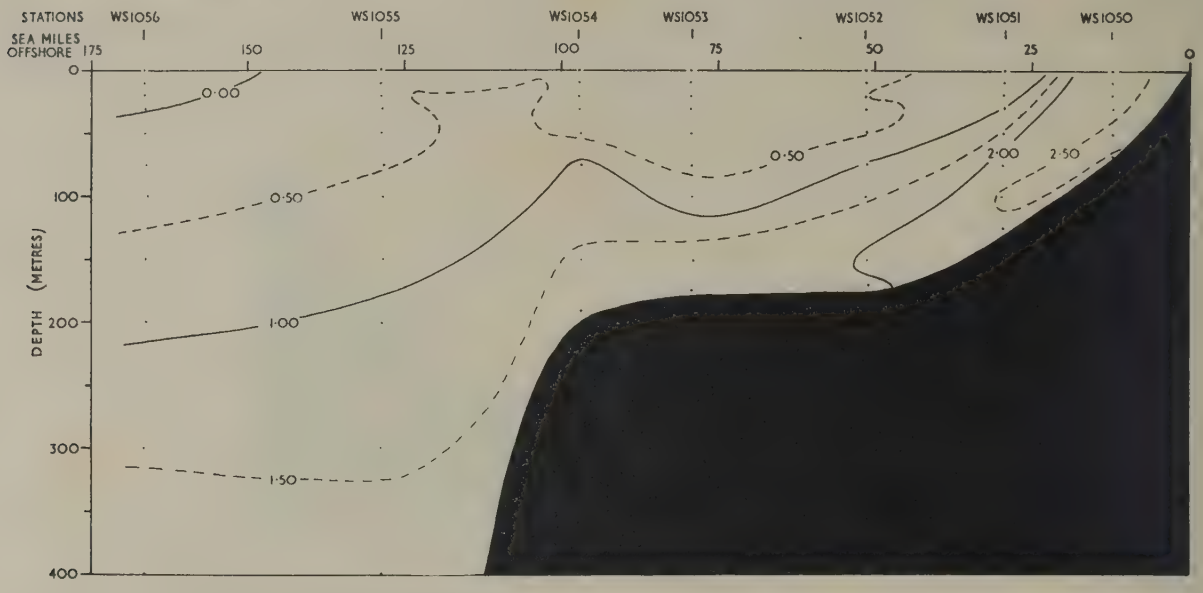

Fig. 53. Distribution of phosphate (mg. ats. P/m.^{3}). Section off the mouth of Orange river, 21–24 September 1950, survey II. Positions of stations are shown in Fig. 2.

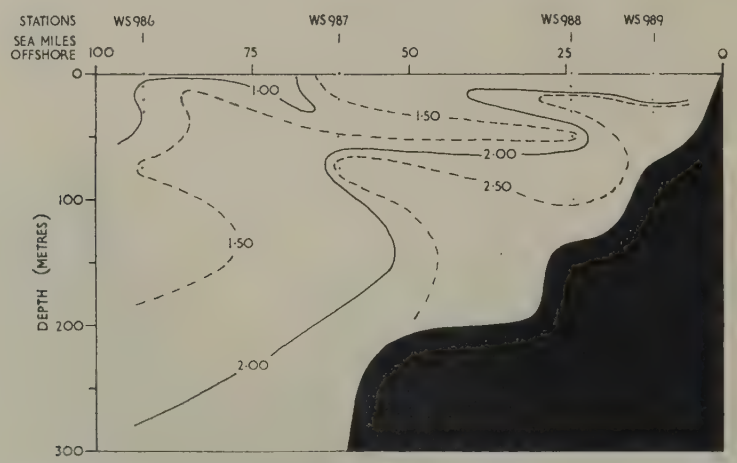

Fig. 54. Distribution of phosphate (mg. ats. P/m.^{3}). Section off Sylvia Hill, 25–27 September 1950, survey II. Positions of stations are shown in Fig. 2.

oxygen minimum layer, and the phosphate concentration more often increases almost regularly to greater depths. The maximum concentration is reached in the antarctic intermediate water.

In the layer of minimal oxygen, however, the inorganic phosphate concentration reaches values of about 2·0 mg. ats. P/m.^{3} With upwelling, this extremely phosphate-rich water is brought up on to the continental shelf, where it provides the necessary nutriment and permits the growth of the heavy crops of phytoplankton in the coastal waters. In several of the sections it will be apparent that the

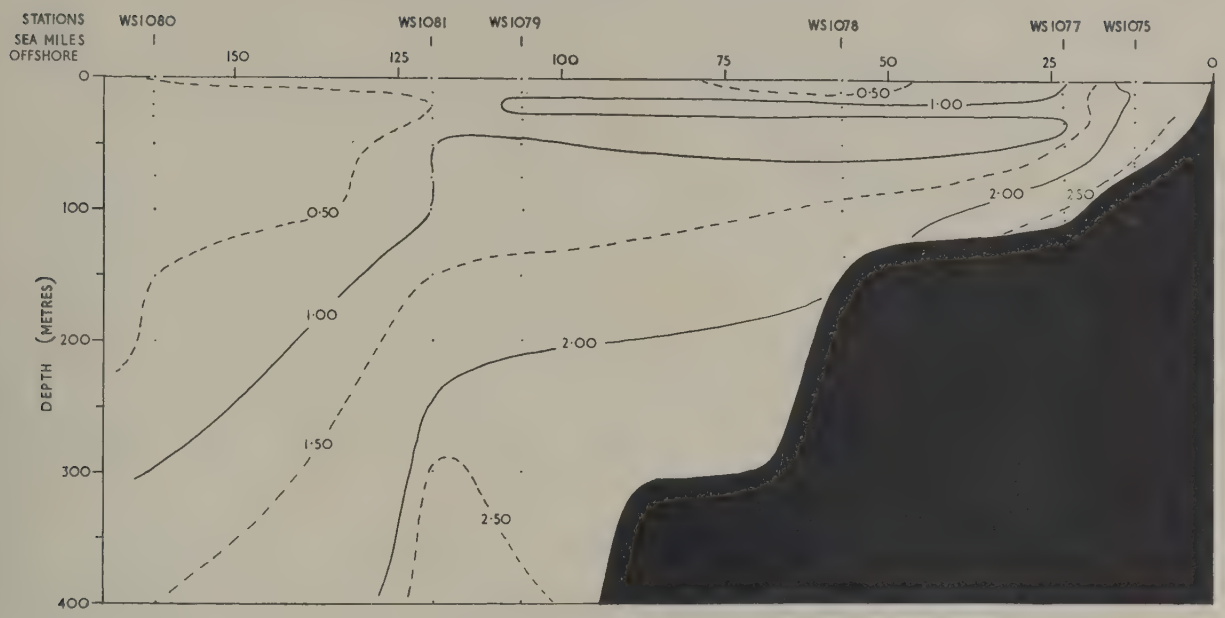

Fig. 55. Distribution of phosphate (mg. ats. P/m.³). Section off Walvis Bay, 29 September–3 October 1950, survey II. Positions of stations are shown in Fig. 2.

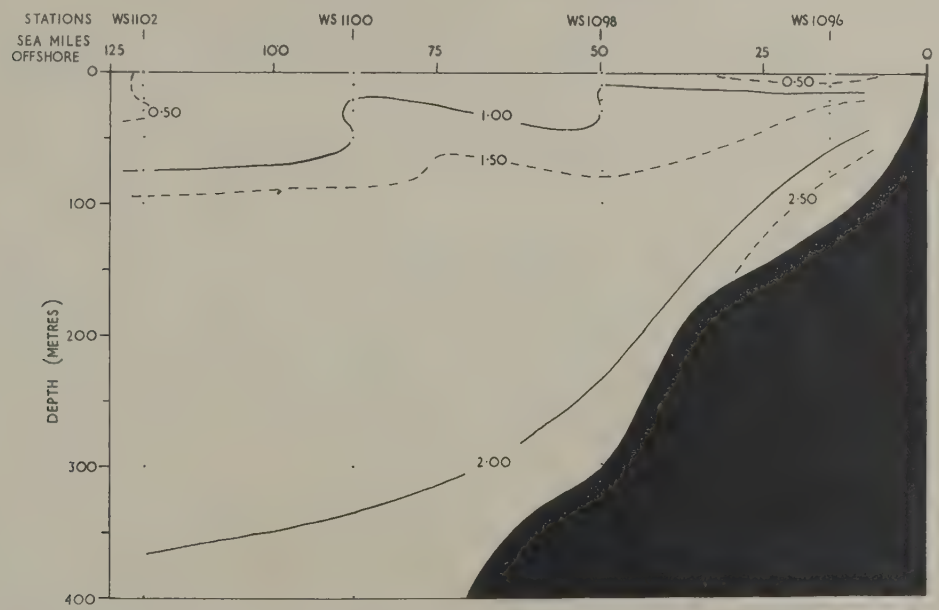

Fig. 56. Distribution of phosphate (mg. ats. P/m.³). Section off Möwe Point, 9–11 October 1950, survey II. Positions of stations are shown in Fig. 2.

phosphate concentration on the continental shelf is higher than that in the water which is being upwelled, and one must attribute this to further enrichment by local decomposition of organic matter on the shelf.

On the Orange river line of survey II (Fig. 53) there is a divergence of phosphate-rich water towards the surface at the edge of the continental shelf. This corresponds with the diverging current which was postulated from the isosteres on this line of stations (Fig. 37).

BOTTOM DEPOSITS

One of the most interesting features of the South-west African region is the presence, on the sea-floor of the continental shelf, of an extensive area of diatomaceous mud. In contrast to the great deposits of diatom ooze which occur in the deep ocean, this zone is confined to shallow waters, and by its very proximity to the sea-surface has made its periodically catastrophic effects all the more evident.

The extent of the diatom mud was outlined by Marchand (1928). He described it as extending principally from 21° 30′ S. to 24° 30′ S. (a distance of about 200 miles) and running seawards for some 25–30 miles from the coast. The bottom samples from this area in his words 'have a green colour and are of a muddy or clayey consistency. The stench emanating from them is unbearable and somewhat similar to hydrogen sulphide or the odour characteristic of putrefaction.'

Close to the coast, however, this mud was not found, and Marchand says that it gives place to a belt of grey sand on which the marine fauna and flora were abundant. It appears, therefore, that the evil smelling mud was confined to an area of the sea-bed between depths of about 50 and 150 m., extending along the coast for some 200 miles.

The absence of marine life in this diatom mud, and the uselessness of the ground for trawling, led to the name by which it is now known, the 'azoic zone' (strictly speaking the name 'anaerobic zone' would be more precise, for the mud does in fact support bacteria and is, therefore, not 'azoic').

Copenhagen (1934) examined the deposits in the azoic zone closely and concluded that the evil smell was in fact hydrogen sulphide, and that it originated from the activities of sulphate-reducing bacteria (Butlin, 1949) which were shown to be present in the sediment. Analyses of the sediment revealed a high content of organic matter and, on drying, a whitish-yellow deposit, evidently of sulphur, became apparent on the surface of the mud.

Microscopical examination of the sediment has shown it to be composed mainly of diatom frustules, although towards the seaward limit of the zone foraminiferal remains become increasingly abundant (Marchand, 1928).

The importance of the azoic zone in the circulation of the waters of the Benguela current became evident when the results of survey I were examined. It was decided, therefore, on survey II to include a series of bottom sampling stations in an attempt to delineate more clearly the total extent of the zone. Samples were taken to the south and to the north of the limits noted by Marchand (1928), and these have shown that the azoic mud extends, at least patchily, for some 400 miles along the coast, from Cunene river mouth (17° 30′ S.) in the north, to about 25° S. Seawards of the deposit is a fairly rapid change to the stone-grey globigerina ooze which characterizes the sediments of the continental slope and floor of the deep ocean to the west.

It is particularly interesting, however, that the azoic mud was not found on the Orange river line, nor in the trawl at station WS 990 on survey I, and this suggests that the southern limit must indeed be somewhere in the region of 25° S. The sediments on the shelf south of the azoic zone do not differ markedly in appearance from the azoic mud, but they have none of the offensive smell of the latter.

Reference to Figs. 38 and 41 shows that over this area the oxygen content of the water overlying the sea-bed, exemplified by the Orange river line, was by no means so depleted as that found, for example, off Walvis Bay over the azoic zone (cf. Figs. 40 and 43). This, in turn, relates to the higher content of dissolved oxygen in the water which was being upwelled on the Orange river line (as shown by the oxygen content at 200–300 m. off the edge of the continental shelf) as compared with that upwelling further to the north.

The evidence, therefore, points strongly to the probability that this diatomaceous sediment to the

south of the azoic zone is maintained in an *aerobic* state by the circulation over it of upwelled water which is not heavily depleted of oxygen.

Another factor, however, which must be considered is that the northerly winds and calms experienced at Walvis Bay (p. 199) do not appear to prevail on the stretch of coast south of 25° S., and their absence may ensure a free circulation of the current over the sediment; but it is felt that these meteorological conditions may concern more implicitly the intensity of the development of the anaerobic region rather than determine the presence or absence of such a zone.

The presence of anaerobic conditions is essential for the growth of sulphate-reducing bacteria, and if the sediment is kept oxygenated they cannot survive.

We have already seen (p. 198) how particular conditions within the current may magnify the effects of hydrogen sulphide production, and indeed at times it is even evolved actively from the sea-surface. There are many observations of bubbles of the gas rising to the sea-surface, but perhaps the following newspaper account gives the most graphic description! (*News Chronicle*, 1938):

SEA GAS ATTACKS TOWN

Swakopmund, the small coastal town in South-west Africa, is undergoing a gas attack set up by continuous submarine disturbances. Heavy sulphurous fumes, especially towards evening, are penetrating as far as 40 miles inland.

Effect. Atmosphere like a London fog, metalwork turned black, public clocks blotted out by deposit, thousands of fish strewn on beach, sharks come into surf gasping on evening tide.

Cause. A geologist, discounting volcanic action, says sulphuretted hydrogen, produced by bacteria on the sea floor from calcium sulphate or gypsum, accumulates until it raises islands of mud, which eventually burst.

In 1951 a particularly active disturbance took place, and on 16 February the *Bulawayo Chronicle* (Anon., 1951*a*) reported:

SEA ERUPTIONS OFF SOUTH-WEST AFRICA

Swakop. S.W.A. Thurs.

The stench of sulphurous sea eruptions pervades the air day and night. Buildings which were white yesterday, are discoloured and black today.

Dead fish are being washed up along the beaches for over 100 miles to the north from Swakopmund. They include many strange species, such as sea snakes and eels, which are found only occasionally when the sea bottom of their habit undergoes violent disturbance.

The sea appears to be boiling with bubbles rising to the surface, but the temperature of the water is only 60°–70° F.

These eruptions continued through March and three mud islands were thrust up in Walvis Bay (Anon., 1951*b*). The largest, about 100 yards long, disappeared overnight.

The islands were similar to one which was thrust up in 1900. Waldron (1910) reported on the latter, from which samples were taken by an officer of a regiment at Walvis Bay, who swam out to the island. The samples were typical of the mud lying on the sea-bed in the bay, and the temperature of the water remained low in spite of the fact that 'steam' was observed to issue from the northern side of the island. The appearance of the island was accompanied by a very strong smell of hydrogen sulphide. As yet no satisfactory explanation of the formation of these islands has been reached.

The importance of the sediment of the azoic zone in yet another way has been emphasized by Brongersma-Sanders (1948) who has shown the significance of this anaerobic deposition of organic matter to oil geology. It is noteworthy how closely the conditions of deposition within this upwelling current parallel those found associated with fossil deposits.

Study of this diatomaceous mud—first distinguished by Neaverson (1934) from the nearly colourless diatomaceous ooze of some deep-sea deposits—may also yield interesting evidence on the silicate

cycle in the sea, by comparison and contrast between the diatom populations found living in the area (the biocoenosis) and the assemblage of forms found in the deposit (the thanatocoenosis). The problems that this type of work may help to solve may even include evidence as to the speed of subsurface currents, as may be seen from the brilliant exposition by Kolbe (1957) working on more specialized samples from very deep waters (cores taken during the Albatross Expedition).

Preliminary examination of our samples from the Walvis Bay line already suggests striking differences between the bottom deposits and the plankton. Of the forms remaining recognizable in the deposits a vastly greater proportion belong to the Discoidae than have yet been recorded in any of the numerous plankton samples from the area of which analyses are now available. That this may be due to much more rapid re-solution of the less strongly silicified forms has been suggested previously on the basis of work in other diatom-rich waters (Hart, 1934, 1942).

MICROPLANKTON

Terminology and presentation of data

The term 'microplankton' is used here to describe the approximate size-limits of the organisms, plant and animal, captured in routine vertical hauls of the N 50 V. These nets were constructed as near to the specification of the $\frac{1}{2}$-m. nets previously used by the 'Discovery Investigations' as post-war materials permitted. The finest bolting-silk obtainable was found to give an approximate mesh size of $40 \times 50\,\mu$ in use. Some few large organisms are present in the catches, and have been tabulated with the others in the summarized results of numerical estimations, but general sampling of the microplankton, more especially of the phytoplankton, was the primary purpose of these hauls.

This definition of the term microplankton agrees with the usages of Sverdrup, Johnson and Fleming (1946, p. 275), based largely on that of Ekmann (1935). They relate the general terms expressive of size limits to methods of capture, thus:

*Macro*plankton: captured by coarse or medium tow-nets.

*Micro*plankton: captured by the finest grade silk nets.

*Nanno*plankton: liable to escape the finest silk, hence also 'centrifuge plankton'. Also studied by using fine filters, sedimentation methods, etc.

The nannoplankton (Lohmann) may be said to include or overlap various groupings of minute forms proposed by more recent specialist workers, such as 'μ-flagellates', 'ultra-plankton' and 'hekisto-plankton' (Cole, 1952).

Though the usage has varied we find that the outstanding plankton workers of the past agree upon the necessity of treating these generally descriptive terms in an elastic manner (cp. Steuer, 1911; Johnstone, Scott and Chadwick, 1924). At first the prefixes macro- and micro- seem to have referred broadly to large plankton organisms visible to the naked eye, and to the host of smaller forms that can be seen with the aid of the microscope. But Johnstone, Scott and Chadwick referred all net-caught plankton to the macroplankton, so that for them microplankton became synonymous with Lohmann's nannoplankton.

Meunier (1913) intended his use of the term microplankton to be construed in the earlier sense, but with restricted application: to unicellular organisms only. This would very nearly meet our needs in discussing the Benguela current material, were it not that the multicellular alga *Trichodesmium* is of some importance among the phytoplankton in that region. Moreover, the relative abundance of the smaller metazoa is obviously an important factor if the 'conditions of life' of the phytoplankton are to be considered.

More recently Ekmann (1953, p. 312), while adhering to his own early definitions (as given by

Sverdrup *et al.*) has added approximate size-limits—60–1100 μ—for the microplankton. Now since Ekmann is dealing with zooplankton this may suit his purpose well enough; but many phytoplankton organisms, especially colonial diatoms, are well sampled by nets, although the individual cells are well below 60 μ in greatest dimensions. The colonial habit permits their retention by the silk, while their highly developed powers of flotation lead to differential settling-rates or actual failure to settle, defeating the centrifuge or reversing-microscope methods of estimating relative abundance, that would otherwise be far more satisfactory than the old net method. The postulation of actual size-limits also brings us up against the fact that in Nature individual species can always be found whose normal range of size-variation bestrides any proposed limit. Many individual species of diatoms and of dinoflagellates normally vary in size from about 35 μ to over 100 μ, and a single important example of a species completely overlapping the proposed upper limit is provided by the well-known *Noctiluca miliaris*. Most samples of this cosmopolitan organism that we have examined, from many parts of the world, have had the majority of individuals ranging between 300 and 600 μ in greatest dimensions, but some frequently attain to 1200 or 1500 μ and have been known to reach 2000 μ (Lebour, 1925, p. 69). Clearly we must admit with Gran (in Murray and Hjort, 1912) and with Johnstone, Scott and Chadwick (1924, p. 75) that '. . . it is impossible to establish clear and absolutely logical distinctions. . .' in the application of these broadly classificatory terms.

This becomes even more obvious when other technical terms, broadly descriptive of aetiological attributes of various categories of plankton organisms, such as those introduced by Haeckel and the Kiel school of planktologists, and by other workers in this field from many countries, come under review (cf. Hart, 1942, p. 268). They are but a part of the jargon without which generalizations cannot be succinctly expressed, and attempts to define them with undue regard to a rigid specialized connotation lead to frustration, because Nature herself seems able to find 'exceptions to every rule'. This obtrusive antithesis should not mean that naturalists must foreswear the ecological point of view. Major types of woodlands, whether defined by foresters or (in somewhat different terms) by terrestrial plant ecologists, are none the less real entities because some kinds of trees are to be found in more than one of them.

This problem of terminology may be partially solved by the growing practice of holding international conferences of recognized leading workers in a given subject, to seek agreement on definitions acceptable to the majority. The alternative is for the individual worker to redefine his own usage when necessary.

The first solution is hampered by language difficulties and the rank growth of 'the literature', such that the richest of languages proves insufficient to provide suitable terms that can be used in specialized connotation, without trespass upon the jargon of some other 'branch of knowledge'. The second, to some extent inescapable, can easily lead one into tedious and unprofitable etymological discussion!

Here we attempt a working compromise by following the usage of Sverdrup, Johnson and Fleming (1946) for most ecological terms. This usage is mainly derived from that of the earlier works mentioned above. When less widely known terms have been employed we have tried to make their meaning plain from the context where they first appear. The meaning of some phrases coined merely for description of the present data will, we hope, prove sufficiently clear if the words are read in their generally accepted, non-specialized sense.

Terms relating more particularly to the phytoplankton are used in the sense that Gran and Braarud (1935) have ascribed to them, as nearly as the differing conditions in this part of the southern hemisphere permit. They have been evolved from the earlier system of 'plankton elements' devised by Gran (1902, 1932) for ecological characterization of the species, during the period when plankton

workers were gradually building up concepts capable of wider application than the older 'plankton types' of Cleve.[1]

Gran's system itself involves the use of some of Haeckel's terminology. 'Holoplanktonic', 'meroplanktonic' and 'tychopelagic', defining the degree to which organisms are dependent on the sea bottom at some period of their history, are widely accepted. 'Oceanic' and 'neritic', however, can soon lead to anachronisms in dealing with the phytoplankton, if applied in a rigidly restricted sense (cf. Hart, 1942, p. 283). Many undoubtedly holoplanktonic 'oceanic' diatoms, to be found in the open sea at all seasons, may attain considerable abundance in coastal ('neritic') sea-areas. Conversely many 'meroplanktonic' (and therefore truly 'neritic') species seem able to go on reproducing vegetatively for so long that they may often form a considerable proportion of the phytoplankton in some 'oceanic' areas far beyond the edge of the shelf.

To avoid the confusion that could arise through the necessity of listing some species as both oceanic and neritic, we suggest the use of the word 'panthalassic' to describe these ubiquitous forms. The word was used by Johnstone, Scott and Chadwick (1924) and is given in *Henderson's Dictionary of Scientific Terms* (1953) as: 'living both in coastal and offshore waters; neritic and oceanic', but we have not yet discovered who first used it in this sense.

To distinguish species of very wide distribution, whether neritic, oceanic or panthalassic, we have here used the adjective 'cosmopolitan' in its general sense, when their known distribution shows a higher degree of tolerance towards temperature and salinity differences than is *necessarily* shown by all the panthalassic species. There are many regions where occupation of both inshore and offshore waters does not involve very wide tolerance of these two best-known parameters of the surface-waters.

Use of the expressions 'dominant' or 'predominant', practically unavoidable in discussing differences between phytoplankton populations, provides another example of the difficulties involved when words so useful in their generally accepted sense acquire an arbitrary, specialized connotation, through the attempt to define them objectively. Numerical preponderance at some arbitrarily chosen level can be misleading (from the point of view of potential productivity) of organisms varying so widely in size and shape, and invites the further criticism that all known counting methods involve errors. Yet, if we are to attempt anything less subjective than the addition of such descriptions as 'abundant', 'common', or 'rare' to the organisms identified, some form of counting—and acceptence of arbitrary levels in drawing deductions from the counts—is unavoidable. Conversely, it should not be forgotten that *admittedly* subjective observations by the earlier naturalists lead to the first recognition of any recurring pattern of plankton distribution.

The whole subject is one to raise echoes of the resounding controversies, as to methods of quantitative plankton investigations, that followed publication of Haeckel's famous *Plankton Studien*, and the replies of Hensen and others, of which the best brief account that we have come across is given by Johnstone (1908).

Throughout the subsequent development of plankton study the early methods have been periodically subjected to destructive criticism, too often by those who have never learnt to count plankton, and constructive reviews like that of Gran (1932) have been few. Considerations which should help to place the matter more fairly in perspective are:

First, the truism that the ideal comprehensive quantitative method may indeed be approached, but

[1] Cleve's 'Plankton Types' constitute the first clear epitome of the close relation between plankton population and conditions of the *milieu*, that may be evident whenever neighbouring water masses are exceptionally well defined. When further work made it clear that water-movements and seasonal changes frequently produced more complicated inter-relationships, it was against the background of Cleve's concept that the new evidence was marshalled. Cleve's 'types' are still distinguishable in essence wherever abrupt differences in environment recur with the consistency usual around southern Scandinavia, but few sea-areas provide such clear-cut examples.

never achieved. Hensen himself had discovered that methods had to be varied to suit the study of different organisms.

Secondly, the necessity for wide, rapid coverage in collection, especially in the less known areas. This often renders crude estimates of relative frequency of greater immediate value than limited series of more accurate data, and was the main reason for our choice of an 'antiquated' method here. The principle is epitomized in Gran's phrase 'a single "absolute" estimation of phytoplankton would be about as valuable as a single temperature determination carried to the third decimal place'.

We have used Hensen's methods for subsampling and counting from routine vertical hauls of the fine silk $\frac{1}{2}$-m. net (N 50 V), but do not follow the early workers in regarding the hauls as representing a constant fraction of the entire contents of the theoretical volume of water filtered. The estimations from counts we regard as roughly comparable indications of relative abundance, within the limits of the very large differences involved in plotting (say) the estimated totals on a logarithmic scale. They are, however, much more accurate as regards the relative importance of species within single samples; and more accurate for small samples than for large ones that have to be diluted to render subsamples small enough to count.

We have found it easier to appreciate the relative frequencies involved by tabulating the actual estimated numbers in primary tables, but in any form of graphic representation it becomes necessary to use logarithmic or other functional ordinates. For the logarithmic reductions we have the classic precedent of Professor Hentschel's work on the 'Meteor' centrifuge-plankton (Hentschel (1936)), and the wide applications of logarithmic scales in dealing with many types of biological data have more recently been well reviewed by Williams (1947). Other scale reductions are indicated on individual diagrams, and it is hoped that sufficient tabular data are included to forestall queries arising from the distortions unavoidable in graphic presentations of this kind.

Recognizing the limitations of these numerical estimates, derived from roughly comparable hauls, the necessity to adopt some arbitrary definition of dominance must still be faced; though we have ventured to retain such useful expressions as 'frequent' and 'important' in their loose, generally accepted sense. Now, the surveys were planned to include observations within two distinct types of surface-water and the boundary region between them. Hence our criterion of dominance must be applicable to individual samples. We cannot, for instance, employ some method like that of Sargent and Walker (1948), who determined most satisfactory levels of significance (on a percentage basis) by pooling results from a whole series of observations. Their method, one of the best we have yet seen, demands, first, that the observations be restricted to a single water mass (though 'succession' with increase in 'age' of the surface-water may be apparent), and, secondly, adequate seasonal coverage; so that 'succession' should not be confused with 'sequence' (i.e. changes in population due to invasion of the area by a different water mass).

Our definition derives direct from the raw data—the estimates of numbers of each category recognized (some 12–50 categories) at each of the eighty-odd stations, arrayed in numerical order from the original counts. We regard the first seven on each list as 'dominant'. By this means the local importance of the more exclusively offshore species is not obliterated by the vast preponderance of the inshore forms, as it would be if the results from the whole of this survey area were pooled. Further, the local importance of some panthalassic species, present in the proportion of (say) 20,000/100,000 at some impoverished offshore station, is not obscured by its presence in greater quantity—perhaps 200,000—at a rich inshore station where the estimated total might be some 200 million, and the first eight or ten categories all exceed two million.

Considering only the thirty-nine stations from each survey that were repeated at approximately the

same positions,[1] this arbitrary choice of a level of 'dominance' was found to show the following results:

(*a*) The lowest (7th) 'dominant' ranged between 0·7 and 7·1% of the estimated total, *mean* 3·5% with σM 1·3. At only two of the seventy-eight stations was its value below 1%, and although the 5% level was exceeded at 8/78 stations, the eighth number of the list (highest category excluded on this scheme) exceeded 5% of the total once only.

(*b*) The sum of the 'dominants', i.e. $\sum_{7\text{th}}^{1\text{st}}$ of the numbers on each list, ranged between 59·8 and 99·6% of the estimated totals, *mean* 81·6% with σM 10. The level fell below 60% at one station only, below 65% at 5/78 stations, and it exceeded 95% at 6/78 stations.

For the four samples of visibly discoloured surface-water, three examined by the drop method and one with the aid of the centrifuge, the 5% level was chosen as the lower limit of 'dominance'.

In the primary tables for the first (autumn) survey the stations numbers are given in chronological order as they were worked, from north to south. During the second survey interpolation of extra stations (mostly for bottom-sampling) and the fact that it was worked from south to north destroys the sequence of the serial numbers. The data have, therefore, been listed so that microplankton data from repeat positions are given in the order in which the corresponding stations had been occupied during the first survey. Although this results in the last becoming first, it should not be confusing because, if the serial numbers are disregarded, it also has the result that observations made in equivalent positions are treated in the same sequence in the Tables for each survey (cf. Figs. 1 and 2, and Tables 14 and 15).

Stations where full series of hydrological and plankton observations were made have been distinguished by printing their serial numbers in ordinary type, while those where only the microplankton net and bathythermograph were used are given in italics.

As an aid to verbal description, the four main lines of observations worked east and west have been named from the most prominent topographical features near their coastal terminations, in order from north to south: the Möwe Point line, Walvis Bay line, Sylvia Hill line and Orange river line. The three lines of subsidiary observations connecting them have been termed the northern, mid- and southern intermediate lines. Approximate mean latitudes for stations worked on each of the four main lines are: Möwe Point line, 19° 40′ S.; Walvis Bay line, 22° 40′ S.; Sylvia Hill line, 25° 20′ S.; and the Orange river line 28° 40′ S.

The order in which groups of organisms, and lesser taxonomic units within the groups, have been arrayed in tables and diagrams, has been governed by the main object of this part of our work: description of the rich microplankton flora as a whole. Strict adherence to the sequence of some recognized scheme of classification would render them very cumbersome and even perhaps misleading, owing to the impracticability of publishing the raw data in full, or of identifying members of all groups down to the same taxonomic level. These difficulties, added to the admittedly unequal sampling of certain groups by the net method, have prompted the following explanation of the relation between our arbitrary arrays and systematic classification, since we have no wish to do violence to systematists' views, whenever they seem well established.

First we give the sequence of main groupings represented in the Benguela current samples, all of which, excepting the silicoflagellata,[2] are usually regarded as classes of algae, according to the classification of Fritsch (1935, 1945)—perhaps the most widely accepted at the present time.

[1] That is omitting the extra stations worked south and north of the main survey area during the second survey.

[2] Fritsch treats the silicoflagellata, whose affinities are still in doubt, as a minor group of uncertain status, at the end of his discussion of the chrysophyceae. We are indebted to Dr M. W. Parke of the M.B.A. Laboratory, Plymouth, for advice on this point.

The five classes out of the eleven considered by Professor Fritsch that were not represented in our material have been omitted. They include the large thallose, attached marine forms, and others with few, if any marine representatives. The sequence of his scheme is indicated by the roman numerals. To each group a summary of the disposition of individual categories (whether species, genera or larger units) that we recorded, has been added:

I Chlorophyceae. With two species of *Trochischia*, rarely and in small numbers only.

II Xanthophyceae. *Halosphaera* only, extremely local.

III Chrysophyceae. With the Coccosphaeriales lumped here because they cannot be adequately sampled by nets (numerically they are a most important group in warmer seas, as nannoplankton methods have shown). *Phaeocystis*, here mercifully less abundant than in colder seas.

Silicoflagellata. With two species, never very abundant but widely distributed.

IV Bacillariophyceae. With ninety-five species or generic categories.

VI Dinophyceae. With forty-two categories, although only the *Ceratia* and a few most obviously important of the other thecate forms were identified down to species.

XI Cyanophyceae. Only one important species here: *Trichodesmium thiebautii*.

From the 'Meteor' results (Hentschel, 1936) we know that the Coccosphaeriales, smaller Dinophyceae and even some of the Chlorophyceae, would figure much more prominently in relation to members of the other groups, if we were considering 'ideal' samples in which nanno- and microplankton forms were represented with equal fairness. On the other hand, *Halosphaera* and the silicoflagellates belong to groups wherein few marine species are known, whatever method of collection is adopted. These limitations, especially those implicit in the choice of the net method, our reasons for which have already been mentioned, led to the decision to treat the phytoplankton under three main headings: Diatoms (Bacillariophyceae), Dinophyceae and 'other Protophyta' or 'other plants'; that is, in descending order of their abundance in these samples, in our main list and primary tables and diagrams.

Within these groups the order of genera adheres to recent systematic practice, though the more detailed description of the diatom flora has involved some arbitrary arrays to be described later.

In the main list the genera of diatoms follow the classification proposed by Hendey (1937), but the species within each genus are arranged alphabetically, because the subgeneric arrangements proposed for some large and important genera are still highly debatable. The Dinophyceae follow the sequence used by Schiller (1933), and the heterogeneous assemblage of 'other plants' the order in which their main groups occur in Fritsch's general classification of the algae.

Chief among the many works consulted for identifications were the Nordisches Plankton series and, for the diatoms, Lebour (1930), Hustedt (1927–37), Hendey (1937) and Boden (1950). For the Dinophyceae, Lebour (1925) and Schiller (1933) were of the greatest assistance.

The Protozoa and Metazoa have been treated less thoroughly than the phytoplankton in these samples because the larger ones were better sampled by coarser nets. The genera of Tintinnoinea were determined with the aid of Kofoid and Campbell's Monograph (1929), but to have done the same for the Radiolaria (equally important at a few stations) was beyond my capacity (T.J.H). Similarly, among the Metazoa, while some individual species of local importance were recorded separately, the Nauplii and other larval categories are quite unequal in systematic status. These diverse groups of animals are listed as nearly to the generally accepted taxonomic order as their nature permits.

The diatoms being by far the most abundant organisms in these samples, are discussed in greater detail than the other main groups, and hence we endeavour to make plain the inter-relations between systematic classification, and arbitrary arrays used merely as an aid to presentation of data, at the outset.

Hendey's classification of the class Bacillariophyceae (diatoms) aims at providing a system wherein the great structural differences between the most abundant plankton forms are more clearly emphasized than they were in earlier systems; among which that of Schütt (1896) with minor modifications by subsequent workers, is still the most widely accepted arrangement.

Schütt's scheme divided the whole group into two suborders Centricae and Pennatae, based upon cell-symmetry around a supposedly central point in the one group, and a more or less iso-bilateral symmetry in the other. Most marine plankton forms belong to the Centricae; and the majority of the attached marine forms, freshwater and soil diatoms to the Pennatae. To this extent the scheme shows a reflection of the earlier ideal, ultimately found impracticable, of classifying diatoms principally upon the mode of life, as Smith (1853–6) had tried to do. The main morphological basis of Schütt's scheme soon shows up the incompatibility: although most of his Pennatae are not to be found as normal constituents of the marine phytoplankton, some lesser subdivisions of the group are well represented therein; so that the agreement between systematic classification based on morphology and primary habitat differences, although better than it is in many other classes of organisms, is by no means complete.

Hendey (1937, 1951) has pointed out that the major subdivisions of the Centricae (variously ranked as sections, families or tribes in later modifications of Schütt's scheme) show structural differences so marked that their inclusion within a single suborder seems questionable. Some of them (Biddulphineae, Soleniineae) even show a type of symmetry that it is very difficult to relate to a supposedly central point. Moreover, even the Pennatae include groups of very diverse structure, although they do not show such extreme divergence from the main characters of the suborder as do some of the Centricae.

Hendey, therefore, proposed that the class Bacillariophyceae, regarded as including only the one order Bacillariales, should be divided into ten suborders of equal systematic status. The first five of these include the forms assigned to various minor rankings in the more recent modifications of Schütt's Centricae (e.g. Hustedt, 1927–37) while the last five were included in Schütt's Pennatae. Hendey (1937) has himself pointed out that with regard to rankings below the level of suborders, his arrangement is not materially different from the earlier ones, and he has been at pains to make due acknowledgement to Schütt and other workers in this field. The formal terminations of the family and subfamily names that he has adopted merely serve to render his classification of the Bacillariophyceae consistent with generally accepted usage among other classes of algae.

Table 11 shows Hendey's classification, excluding the genera not represented in the material that he was working on when he first formulated it. That material consisted of a large selection of plankton samples from most of the areas traversed by ships of the Discovery Investigations in the Southern Hemisphere, prior to 1935.

In Table 11 the genera and corresponding supra-generic rankings observed in our Benguela current material have been printed in ordinary type, leaving the groups that have as yet been recorded only from other parts of southern seas distinguished by italics.

Supra-generic rankings, either at the level of suborder or family, were found to lend themselves to the definition of four of the five arbitrary groupings used later in this report, for descriptive purposes only. They are preceded by numbers in brackets, and printed in bold type in Table 11.

The fifth group is a lumping of such members of the last five of Hendey's suborders as occurred in the Benguela current samples. In this report they have been termed 'Pennatae' for the sake of brevity *not* from any desire to revert to the older classification.

Whether one thinks of them as the Pennatae of Schütt, or the last five suborders of Hendey's system, those familiar with marine phytoplankton will know that nearly all the planktonic members

Table 11. *Classification of plankton diatoms proposed by Hendey (1937) with the genera and higher groups seen in the Benguela current material in ordinary type, others in italics. Note: this is not a complete classification, many non-marine or non-planktonic genera having been omitted. Inclusion of all diatom genera would slightly alter the sequence of some of the units of less than sub-ordinal rank.*

The first four of the five arbitrary groupings used for descriptive summaries in this report coincide with suborders or families in the system, and are shown below in heavy type. The fifth group, a heterogeneous lumping from the last five suborders, has been termed 'pennatae' for the sake of brevity, but is not intended to imply reversion to earlier classification (see text)

Sub-orders	*Families*	*Sub-families*	*Genera*
DISCINEAE			
	Coscinodiscaceae		
		Melosiroideae	
			Melosira
			Hyalodiscus
		Skeletonemoideae	
			Skeletonema
			Stephanopyxis
			Detonula
		Thalassiosiroideae	
			Thalassiosira
			Coscinosira
			Lauderia
			Schröderella
			Bacterosira
		Coscinodiscoideae	
			Coscinodiscus
			Charcotia
			Planktoniella
			Gossleriella
			Schimperiella
			Actinocyclus
	Hemidiscaceae		
		Hemidiscoideae	
			Hemidiscus
	Actinodiscaceae		
		Stictodiscoideae	
			Stictodiscus
			Arachnoidiscus
		Actinoptychoideae	
			Actinoptychus
		Asterolamproideae	
			Asterolampra
			Asteromphalus
AULACODISCINEAE			
	Eupodiscaceae		
		Pyrgodiscoideae	
			Pyrgodiscus
		Aulacodiscoideae	
			Aulacodiscus
		Eupodiscoideae	
			Eupodiscus
AULISCINEAE			
	Auliscaceae		
		Auliscoideae	
			Auliscus
BIDDULPHIINEAE			
	Biddulphiaceae		
		Biddulphioideae	
			Biddulphia
			Bellerochea
			Cerataulus
			Cerataulina
		Triceratioideae	
			Triceratium
			Trigonium
			Pseudotriceratium
			Lithodesmium
			Ditylum
		Hemiauloideae	
			Hemiaulus
		Eucamphioideae	
			Eucampia
			Streptotheca
			Climacodium
	Anaulaceae		
		Anauloideae	
			Anaulus
	Chaetoceraceae		
		Chaetoceroideae	
			Chaetoceros
SOLENIINEAE			
	Bacteriastraceae		
		Bacteriastroideae	
			Bacteriastrum
	Rhizosoleniaceae		
		Rhizosolenioideae	
			Rhizosolenia
			Guinardia
	Leptocylindraceae		
		Leptocylindroideae	
			Dactyliosolen
			Leptocylindrus
	Corethronaceae		
		Corethronoideae	
			Corethron
ARAPHIDINEAE			
	Fragilariaceae		
		Fragilarioideae	
			Fragilaria
			Fragilariopsis
			Asterionella
			Synedra
			Thalassionema
			Thalassiothrix
		Meridionoideae	
			Meridion
		Tabellarioideae	
			Licmophora
			Grammatophora
			Striatella
			Rhabdonema
			Entopyla
RAPHIDIOIDINEAE			
	Eunotiaceae		
			Eunotia
MONORAPHIDINEAE			
	Achnanthaceae		
		Achnanthoideae	
			Achnanthes
		Cocconeioideae	
			Cocconeis
BIRAPHIDINEAE			
	Naviculaceae		
		Naviculoideae	
			Navicula
			Trachyneis
			Scoresbya
			Pleurosigma
		Amphiproroideae	
			Amphiprora
			Tropidoneis
	Gomphonemaceae		
		Gomphonemoideae	
			Gomphonema
	Cymbellaceae		
		Cymbelloideae	
			Cymbella
			Amphora
	Epithemiaceae		
		Epithemioideae	
			Epithemia
	Bacillariaceae		
		Nitzschioideae	
			Nitzschia
			Chunella
		Bacillarioideae	
			Bacillaria
SURIRELLINEAE			
	Surirellaceae		
		Surirelloideae	
			Surirella
		Campylodiscoideae	
			Campylodiscus

of this group belong to the two families Fragilariaceae and Naviculaceae, with a few species of the genus *Nitzschia*. These forms, which fall into the suborders Araphidineae and Biraphidineae of Hendey's system, exhibit features that fit them for a free-floating existence (if the teleological expression may be forgiven). Such features are the development of catenary, branching or ribbon-forming colonies; attenuated form of the individual cells; or the possession of cell-walls much slighter than those of their bottom-dwelling relatives. Indeed, in an aetiological sense, they have collectively been well described as 'reversionary plankton forms', by Lloyd (1926). However, in this material, as in that from other coastal areas, we find that a small proportion of bottom-dwelling forms (e.g. *Achnanthes* which falls within Hendey's Monoraphidineae) occur tychopelagically in the plankton. In need of a summary group-heading that would include these also, it was felt that the old term 'Pennatae', though of doubtful value in its taxonomic sense, would be more convenient than some cumbersome phrase such as 'last five suborders'. The expression 'small pennate diatoms' that Marshall (1933) found convenient for ecological description of material from the Great Barrier Reef, is only a partial equivalent, since large species like *Thalassiothrix longissima* and *Pleurosigma capense* are included in the Benguela grouping.

For the rest, Hendey's suborder Discineae suited our purpose well as it stands, but coming to the suborder Biddulphineae it seemed best to divide the outstandingly abundant Chaetocerids from the others at family level, for the latter derive from several subfamilies, whereas the Chaetoceraceae include but the one subfamily, and indeed, in this material, only the one genus. The Soleniineae, consisting almost exclusively of holoplanktonic forms, provided a convenient grouping at the level of the suborder.

Thus four of our five arbitrary groupings can be defined in terms of widely accepted systematic assemblages, though these are not of equal status. The fifth group remains heterogeneous. Abstracting them from the classification table, and summarizing their main ecological characteristics, we have:

I Suborder **Discineae**. Most of the species neritic and probably meroplanktonic, with heavily silicified frustules. Exceptions (holoplanktonic, relatively more abundant in the sparser phytoplankton at greater distances from land) were *some* of the *Thalassiosira* spp. and the definitely oceanic *Planktoniella*. The colonial habit and gelatinous or spiny projections of the former, and thin, hyaline, ribbed extensions of the valve margins of the latter, may conceivably assist flotation.

II Family **Biddulphiaceae**. Mainly neritic, few solitary, but the others showing very varied development of the colonial habit. A few are oceanic, holoplanktonic (very rare in these samples, e.g. *Hemiaulus Hauckii*). Majority meroplanktonic (*Eucampia*, *Biddulphia*) or even bottom-dwelling species (*Triceratium*) whose occasional presence alive in the plankton may justify their inclusion as tychopelagic species.

III Family **Chaetoceraceae**. Mainly holoplanktonic in the vegetative phases, but a majority form specialized resting spores and are, therefore, probably meroplanktonic. Many neritic, few oceanic species. In comparison with II, with which they form the suborder Biddulphiineae, the Chaetoceraceae show an increased development of structural features that must tend to aid flotation: thin, less strongly silicified frustules, and horns produced into long setae. Mainly colonial.

IV Suborder **Soleniineae**. Nearly all holoplanktonic, many oceanic or panthalassic, few neritic. Structurally they include large and medium-sized tubular species, solitary or in colonies of few cells and long chains of small cylindrical species.

V 'Pennatae'. A heterogeneous arbitrary grouping, as explained in detail above. It consists of the few normally planktonic members of Hendey's Araphidineae and Biraphidineae (the 'reversionary plankton forms' of Lloyd) with such few bottom-dwelling forms from the last five of Hendey's sub-

orders (Pennatae proper, if one prefers Schütt's system) as were found to occur tychopelagically in these samples. Mainly meroplanktonic, neritic.

Taxonomic notes

Changes in nomenclature of phytoplankton species have been adopted where recent taxonomic research seems to justify them. Most of these are better known to plankton workers under earlier names current in general handbooks such as Engler and Prantl's *Pflanzenfamilien*, the Nordisches Plankton series and M. V. Lebour's *Planktonic Diatoms of Northern Seas*. It is hoped that these notes may prevent further confusion. They give first the name used in this report in bold type, the best known previous synonym, and then the authority for the change. *Full* synonymy is *not* attempted here. Some brief comment has been offered concerning changes that still seem to the writer to be of doubtful value, but detailed taxonomic study would require a separate report. (Where the first person has been used in this section the opinions expressed are those held by one of us (T. J. H.) personally.)

Hemidiscus cuneiformis Wallich (1860), formerly *Euodia cuneiformis* (Wallich) or *E. cuneiformis* Schütt.

Hustedt (1927–37, p. 903) and Hendey (1937, p. 264) have explained how the foundation of several species that they believe to be but varieties or phases of the type, coupled with Castracane's error in supposing that *Euodia* Bailey, 1861, predated Wallich's foundation of the genus *Hemidiscus*, has led to prolonged uncertainty as to the correct naming of this species. It is interesting to note that in all the welter of confusion Cleve (1901, p. 330) had worked back to the combination now considered correct, although he later supported Gran's use of *Euodia cuneiformis* (Wallich) as synonymous with *E. gibba* Bailey (Gran, 1905, p. 45).

Actinoptychus senarius Ehrenberg, previously widely known as *A. undulatus* (Bailey). Hendey (1937, pp. 271–2) shows that Ehrenberg's specific name should be adopted upon grounds of priority. Confusion arose because Ehrenberg first described it as a species of *Actinocyclus* (Ehrenberg, 1838). Later he himself recognized the structural differences that seemed to warrant the splitting of this genus into *Actinocyclus* as most subsequent workers have known it, and *Actinoptychus* which he established as a distinct genus, with *A. senarius* as the type-species (Ehrenberg, 1841, 1843). The figures of this form given as an unnamed species of *Actinocyclus* by Bailey (1842) first received the specific epithet *undulatus* from Kützing (1844), and the combination *Actinoptychus undulatus* (Bailey) was made by Ralfs in the fourth edition of Pritchard's *History of the Infusoria*, 1861! Ehrenberg himself seems to have had no doubt that the unnamed figure of *Actinocyclus* sp. given by Bailey, and later called *Actinocyclus undulatus* by Kützing, was specifically indentical with his own '*Actinocyclus*' (later *Actinoptychus*) *senarius* (Ehrenberg, 1843, p. 328).

Cerataulina pelagica (Cleve) Hendey comb. nov., more widely known as *C. Bergonii* H. Peragallo or *Cerataulus* (*Cerataulina*) *Bergonii* (H. Peragallo).

Hendey (1937, p. 279) states that though Peragallo first suggested the need for a new genus (*Cerataulina*) when he described the species *Cerataulus* (*Cerataulina*) *Bergonii* H. Peragallo (1892), he did not define that genus. Later it appears that Cleve (1894, p. 11) accepted Peragallo's tentatively proposed name, while pointing out that the form which he had himself described earlier as *Zygoceros pelagicum* (Cleve, 1889, p. 54) was a complete synonym. Yet the genus *Cerataulina* does not seem to have been properly established anywhere until Schütt's publication of 1896 (in Engler and Prantl, p. 95). Hendey's proposed combination seems the only means of bringing the species within the bounds of accepted rules of nomenclature, though plankton workers have been familiar with '*C. Bergonii*' for so long that they cannot but regret the change.

Chaetoceros atlanticum var. (or phase) **neapolitana (Schröder) Hustedt**, previously often regarded as a distinct species, *C. neapolitana* Schröder. Here lumped with the type.

Gran and Yendo (1914) noted that this form, which they regarded as a distinct species, was most often to be found in the warmer waters around Japan, while the highly variable and cosmopolitan *C. atlanticum* Cleve was mainly confined to the colder water masses in that region. Earlier work round Japan suggests that the *neapolitana* form might be found in the colder waters also. Though Okamura (1907) identified his specimens as *C. atlanticum*, Gran and Yendo seem satisfied that they were the *neapolitana* form, and doubted the localities whence they were recorded in consequence!

Hustedt (1927–37), Hendey (1937) and Boden (1950), the latter working on South African material, have regarded *neapolitana* as a variety of *C. atlanticum*. It was Hustedt who regularized this change, and both he and Hendey also dealt with the very confused synonymy of the type.

Our material seems clearly to support the view that *neapolitana* can hardly be a separate species. Both the type (*C. atlanticum*) and the variety occurred together at some stations near the shelf-edge, with seemingly intermediate forms, and *neapolitana* more frequently than type or intermediates in the warmer oceanic water still farther offshore.

The regular banded appearance of the setae, due to chloroplasts penetrating into them and disposed at regular intervals, was very characteristic of the *neapolitana* phase, and is shown in figures of material from other localities by Schröder himself (1900) and Cupp (1943) among others. However, our material also showed individual colonies of both type and intermediates with a similar disposition of chloroplasts. We have to remember that the movements of chloroplasts within the shell are probably governed by light intensity. Hence this appearance in preserved samples may depend more upon the depth at which they were captured and time interval prior to fixation than upon any greater tendency towards this pattern in the *neapolitanum* phase, rather than in type or 'intermediate' strains.

Certainly we would agree with Gran and Yendo that *neapolitana* is a warm-water phase of the species, and this is also the view of Cupp (1943) and Takano (1954) who gives excellent figures of what he terms var. *neapolitana* and var. *skeleton*.

It seems significant to me that when material from the north-eastern Atlantic only has been studied, there are many examples of diatoms that show a polymorphism, seemingly so definitely related to temperatures (and therefore having a distinctive space/time distribution) that systematists have failed to agree upon the specific or subspecific status of the different forms. Yet, when material from regions with steeper temperature gradients has been examined, these same cosmopolitan diatoms have seemed to fall much more convincingly into categories of less than specific rank (often obviously linked by intermediate forms) of single types. Thus these chaetocerids, and the solenoids mentioned below, seem justifiably 'lumped' on the basis of our Benguela current material, derived from a typical upwelling region where the temperature gradients are frequently very steep. Such abrupt variations in temperature are also to be found near the northern limits of the Kuroshiwo current, whence some of Gran and Yendo's material and most of Takano's was derived.

Chaetoceros costatum Pavillard, previously widely referred to as *C. adhaerens* Mangin.

This change was advocated by Hustedt (1927–37, pp. 699–700). Its propriety is not very obvious from the figures he reproduced from Pavillard and from Mangin. Cupp (1943, p. 127) follows Hustedt and gives better figures, that agree well with the varied South-west African samples we studied.

In our material the species was very restricted in distribution, but abundant at four autumn stations inshore. Here the range of variation in dimensions coupled with the presence of mucous (or 'pectinaceous') cushions between corners of adjoining cells, a character of Mangin's definition, in chains that also displayed the intercalary bands shown by Pavillard's figure, led me to conclude that Hustedt

is correct in accepting Pavillard's specific name on grounds of priority (Pavillard, 1911, p. 24, fig. 1*b*, *c*; Mangin, 1912, p. 39, fig. 25, pl. II, fig. 10).

The intercalary bands arranged in imbricating fashion were hard to see in some of the colonies, and many of the frustules resemble the two lower ones in Pavillard's figure, where the bands are visible only where they approach the cell margin as seen in broad girdle view. Such banding on the connective zone is a rare feature among Chaetocerids, viewed under ordinary conditions, but characteristic of the related genus *Attheya*.[1]

Some of our material even suggested that *Chaetoceros imbricatus* Mangin (1912, fig. 37) should also perhaps be considered as a synonym of *C. costatum* Pavillard, the cells in the chains were so closely adpressed, but I could not feel sure of distinguishing between these forms and phases of *C. didymum* like the var. *agregata* also figured by Mangin (1912, fig. 37) from the type locality of his *C. imbricatus* off Brest, under the working conditions imposed by normal plankton analysis. *C. didymum* was exceedingly abundant, in a welter of varieties or phases, at most inshore stations during our Benguela current survey. The question must be left open, with the admission that further detailed work may serve to show the presence of *C. imbricatus* Mangin here, and that it may have been wrongly included with *C. costatum* Pavillard, or with some phase of *C. didymum* in my counts. As the numbers involved were exceedingly small in comparison with those of clearly indentifiable species, the point is of small moment in considering the diatom flora as a whole.

Chaetoceros subsecundum (Grunow) Hustedt formerly known as *Chaetoceros diadema* (Ehrb.) Gran.

Hustedt (1927–37, p. 645) details the argument by which, under the International Rules for Botanical Nomenclature, the widely known specific name *diadema*, finely descriptive of the resting spores, and based on *Syndendrium diadema* Ehrenberg 1854, should be supplanted by the above combination, based on *C. distans* (Cleve) var. *subsecunda* Grunow (ex Van Heurck, 1881 (1880–5).

It appears that Grunow was right to reject *diadema* on realizing that the forms in question were related to *Chaetoceros*, *Syndendrium diadema* becoming a *nomen confusem*, since it was based upon the resting spores only. Unfortunately, Grunow was mistaken in relating it to *C. distans* Cleve (1873), itself a misidentification of *C. dichaeta* Ehrenberg. It thus became necessary to elevate the varietal name to specific rank as Hustedt has done, though there is still much doubt and confusion about the full synonymy.

I am greatly indebted to Mr N. I. Hendey for a personal communication helping to clear up this obscurity.

Rhizosolenia imbricata Brightwell var. (or phase) **Shrubsolei Cleve**, often previously considered as a distinct species, *R. shrubsolei* Cleve.

Our Benguela material of this usually small and narrow form of comparatively cold waters seems to me to provide ample support for the view that it is not specifically distinguishable from the stouter form of warmer seas described as *R. imbricata* by Brightwell.

Hustedt (1927–37, p. 584) gives formal expression to this view, and points to the synonymy with *R. striata* Greville and the apparent lack of justification for the establishment of Peragallo's *R. atlantica* and *R. pacifica*, both seemingly also synonyms of *R. imbricata* Brightwell.

A footnote of Gran's (1905, p. 52) anticipates Hustedt's decision, pointing out that if the specific identity of the two forms could be demonstrated, Brightwell's name should be the one used on priority grounds, and it would seem that Cleve himself had drawn attention to the matter.

At several Benguela current stations both forms were present, mainly very much as figured by Lebour (1930, p. 97) under the name *R. shrubsolei* Cleve, but many individuals intermediate both with

[1] Intercalary bands have also been described in *Chaetoceros teres*, visible only after special treatment and mounting (Mangin, 1908) and in *Chaetoceros eibenii* by Pavillard (1921).

regard to their size and degree of flattening of the valves were also present. Also I gained a distinct impression of a relative increase in numbers of the stouter form in the warmer waters *before* re-reading the debatable taxonomic literature.

Boden (1950) who worked on material from the Atlantic side of Cape Peninsula has also accepted Hustedt's view, but a full study of the earlier synonymy and detailed re-examination of our material in further support thereof would require a separate publication.

Fragilaria Karsteni Boden *nom. nov.* instead of *F. capensis* Karsten.

Boden (1950, p. 406) has explained that Karsten's term was preoccupied by *F. capensis* Grunow, 1863, which differs structurally and in size from the species under discussion, hence the need for the new name that Boden has established.

Thalassionema nitzschioides (Grunow) Hustedt, previously very widely known as *Thalassiothrix nitzschioides* Grun., Van Heurck.

Hendey (1937, p. 336) points out that although Grunow wrote of the possibility of a need to establish a new genus *Thalassionema* he did not define this proposed genus at all, and that Hustedt (1927–37, p. 244) was the first to do so. Hendey holds, therefore, that the authority should be ascribed to Hustedt.

Noctiluca miliaris Suriray, instead of *N. scintillans* (Macartney) to which this widely known organism is often referred.

On this vexed question we have accepted Schillers (1933–7) verdict in favour of the later *N. miliaris* Suriray (1816), 1836, against the earlier synonyms *Medusa marina* Slabber (1771) 1778, and *Medusa scintillans* Macartney, 1810. Kofoid (1919) who first produced good evidence of the dinoflagellate affinities of this enigmatic, heterotrophic form, preferred Macartney's specific name for it. Before that most marine biologists had used *Noctiluca miliaris* Suriray.

We have not been able to consult all the early references quoted by Schiller, but if the genus *Noctiluca* of Suriray is accepted, as it has been by almost all naturalists ever since Ehrenberg used it in 1834, it seems only consistent to use his specific name for the type-species also; since the earlier synonyms placed the organism in a 'false genus'. Under admittedly much more recent interpretations of the 'rules of nomenclature', they should therefore lapse; unless Suriray had himself decided to use one or the other in making a 'new Combination'. Most probably he did not know of the earlier descriptions.

Dinophysis tripos Gourret, previously widely known as *Dinophysis homunculus* var. *tripos* (Gourret).

It is now generally held that Stein's *D. homunculus* is a synonym, in part, of at least three of the species in the Caudata group of *Dinophysis: D. caudata* Kent, which should replace *homunculus* as a specific and as group-name on grounds of priority, *D. diegensis* Kofoid and *D. tripos* Gourret. Lebour (1925) has pointed out that in *D. tripos* the hypotheca always shows a second smaller more dorsal point, in addition to the well-defined 'Tail'; whereas in *D. caudata* varieties the tendency to form a definite projection in the corresponding position is much less pronounced. A single figure of an extreme variety of *D. caudata* from the Persian Gulf by Dr V. Pietschmann, reproduced by Schiller (1933, p. 157, f. 145, u.) shows a definite secondary 'point', but it is appreciably smaller and less acute than that of *D. tripos*, even when comparing it with the figures of the latter (several are given by Schiller) in which the feature is least developed. 'Discovery' material both from the east and west coasts of Africa seemed to me (T. J. H.) to be clearly ascribable to *D. tripos* Gourret, although *D. caudata* Kent may also be found at some of the localities.

In the Benguela current, *D. tripos* was limited to the extreme north of the area covered by our survey, and to the extra stations south of the area that preceded the second survey. It was not observed in the central portion of the coastal current where the heaviest diatom catches were taken and where

the negative temperature anomaly was greatest. This can scarcely be due to the effect of temperature, however, for the species is often abundant in water as cold as this (in the absolute sense, not in terms of iso-anomaly) far to the south on the Atlantic side of Cape Peninsula. Further, it may be equally abundant in warm waters of the Agulhas current on the east coast, as far north as Durban and probably beyond. This implies temperature tolerance throughout the range 10° to 23° C. at the least. The discontinuity in distribution off the south-west coast could, however, be due to a markedly stenohaline reaction on the part of *D. tripos*. The area from which we found it almost absent coincides with the low salinities observed northwards from the Orange river mouth throughout the area of maximum upwelling activity to Luderitz Bay and beyond.[1]

The point has been mentioned here because Schiller (1933) who has done so much to clear up the taxonomy of the Caudata group, added the trenchant note 'Ob immer stenohaline?' concerning the distribution of *D. tripos*, which suggests that this trait had already been noticed in other regions.

Diversity of the microplankton

The rich variety of the microplankton in the region surveyed may be judged from the list of all 208 categories recorded in the routine counts (Table 12). This table also shows their frequency of occurrence, and the frequency with which they occurred as dominants in each of the two separate series of thirty-nine stations, repeated at approximately the same positions, and in the smaller subsidiary series as shown by the column headings.

Table 12. *List of all microplankton categories recorded among routine counts, with data on their frequency of occurrence, and dominance, as shown by column headings*

	First survey 39 stations		*Second survey 39 stations (repeated)*		*Six extra stations to south of main area*		*Three extra stations to north of main area*		*Four discoloured water-samples*		*Station WS 1076 (extra, no counterpart on first survey)*	
Species or category	*Present*	*Dominant*	*Present*	*Dominant*	*Present*	*Dominant*	*Present*	*Dominant*	*Present*	*>5%*	*Present*	*Dominant*
Diatomacea												
Melosira sphaerica Karsten	2	—	—	—	—	—	—	—	—	—	—	—
Skeletonema costatum (Grev.) Cleve	1	0	3	1	—	—	—	—	—	—	—	—
Stephanopyxis palmeriana (Grev.) Grünow	—	—	—	—	1	—	—	—	—	—	—	—
S. turris (Grev. & Arnott) Ralfs	10	3	11	1	3	1	1	0	3	0	—	—
Thalassiosira condensata Cleve	5	0	—	—	4	2	1	1	—	—	—	—
T. excentrica Karsten	14	3	3	1	—	—	—	—	—	—	—	—
T. hyalinum (Grün.) Gran	4	0	—	—	—	—	—	—	—	—	—	—
T. rotula Meunier	1	0	—	—	—	—	—	—	—	—	—	—
T. subtilis (Ostenfeld) Gran	12	2	14	3	4	4	—	—	—	—	—	—
Thalassiosira spp. non det.	2	0	14	5	2	0	3	1	3	0	1	0
Bacterosira fragilis Gran	1	0	—	—	—	—	—	—	—	—	—	—
Coscinodiscus gigas Ehrenberg	1	0	—	—	1	0	—	—	—	—	—	—
C. janischii A. Schmidt	1	0	—	—	2	0	—	—	—	—	—	—
C. parvulus Karsten	1	0	—	—	—	—	—	—	—	—	—	—
C. radiatus Ehrenberg	1	0	—	—	—	—	—	—	—	—	—	—
Coscinodiscus spp. non det.	8	0	28	1	3	0	2	0	1	0	1	0
Actinocyclus spp. non det.	2	0	—	—	—	—	—	—	—	—	—	—
Planktoniella sol Wallich	19	6	24	9	6	1	2	0	—	—	—	—
Hemidiscus cuneiformis Wallich	1	0	2	0	—	—	2	0	—	—	—	—
Actinoptychus senarius Ehrenberg	2	0	6	0	—	—	2	0	—	—	1	0
Asterolampra spp. non det.	—	—	1	0	—	—	—	—	—	—	—	—
Asteromphalus heptactis (Brebisson) Ralfs	5	0	6	1	—	—	—	—	—	—	—	—
Biddulphia longicruris Greville	—	—	6	0	1	0	—	—	—	—	—	—
B. mobiliensis Bailey	—	—	—	—	2	0	—	—	—	—	—	—
B. regia (Schultze) Ostenfeld	—	—	—	—	1	0	1	0	—	—	—	—
Cerataulina pelagica (Cleve) Hendey	3	0	1	0	—	—	1	0	—	—	—	—
Triceratium favus Ehrenberg	1	0	—	—	1	0	—	—	—	—	—	—
Triceratium spp. non det.	—	—	—	—	1	0	—	—	—	—	—	—

[1] Here Dietrich (1950) has shown iso-lines of negative anomaly of 0·5–1·5 ‰ salinity, with normal values north and south, and but a little distance seaward.

Table 12 (*cont.*)

Species or category	*First survey 39 stations* Present	Dominant	*Second survey 39 stations (repeated)* Present	Dominant	*Six extra stations to south of main area* Present	Dominant	*Three extra stations to north of main area* Present	Dominant	*Four discoloured water-samples* Present	>5%	*Station WS 1076 (extra, no counterpart on first survey)* Present	Dominant
DIATOMACEA												
Ditylum brightwelli (West) Grünow	—	—	—	—	6	1	—	—	—	—	—	—
Hemialus hauckii Grünow	1	0	—	—	—	—	—	—	—	—	—	—
Eucampia cornuta (Cleve) Grünow	—	—	2	0	—	—	—	—	—	—	—	—
E. zoodiacus Ehrenberg	11	4	—	—	3	0	—	—	3	0	—	—
Chaetoceros affine Lauder	2	1	4	1	2	1	—	—	—	—	—	—
C. atlanticum Cleve	—	—	15	5	—	—	1	0	1	0	—	—
C. compressum Lauder	17	13	22	14	4	3	2	2	1	0	1	0
C. constrictum Gran	22	12	26	19	2	2	3	1	2	0	1	1
C. convolutum Castracane	17	7	22	5	5	0	2	1	—	—	—	—
C. costatum Pavilliard	4	4	1	0	—	—	—	—	—	—	1	0
C. curvatum Castracane	2	0	—	—	—	—	—	—	—	—	—	—
C. curvisetum Cleve	15	11	18	12	4	3	2	2	1	0	1	1
C. debile Cleve	4	3	4	2	1	1	—	—	—	—	1	1
C. decipiens Cleve	5	1	14	8	4	0	—	—	—	—	1	0
C. densum Cleve	—	—	—	—	—	—	—	—	—	—	1	0
C. difficile Cleve	8	5	4	2	—	—	—	—	—	—	—	—
C. didymum Ehrenberg (vegetative phases)	12	6	10	2	1	0	2	1	1	0	—	—
C. didymum Ehrenberg (resting spores)	13	6	3	0	—	—	—	—	—	—	1	0
C. holsaticum Schütt	—	—	3	0	—	—	—	—	—	—	—	—
C. imbricatum Mangin	1	0	—	—	—	—	—	—	—	—	—	—
C. laciniosum Sthütt	1	0	1	0	—	—	—	—	—	—	—	—
C. lorenzianum Grünow	2	0	14	9	—	—	2	1	—	—	—	—
C. parallelis Boden	—	—	1	0	—	—	—	—	—	—	—	—
C. peruvianum Brightwell	8	0	10	1	1	0	—	—	—	—	—	—
C. pseudocrinitum Ostenfeld	2	1	—	—	—	—	—	—	—	—	—	—
C. sociale Lauder	1	0	5	3	—	—	—	—	—	—	1	1
C. strictum Karsten	11	7	10	6	1	0	1	0	—	—	—	—
C. subsecundum (Grün.) Hustedt	11	3	3	0	—	—	—	—	—	—	—	—
C. subsecundum (Grün.) Hustedt (resting spores)	3	0	—	—	—	—	—	—	—	—	—	—
C. teres Cleve	15	7	2	0	—	—	—	—	—	—	—	—
C. tetras Karsten	4	1	2	2	—	—	—	—	—	—	—	—
C. van heurckii Gran	9	5	1	0	1	0	—	—	—	—	—	—
Chaetoceros spp. non det.	3	2	—	—	—	—	—	—	—	—	—	—
Bacteriastrum delicatulum Cleve	—	—	—	—	1	0	—	—	—	—	—	—
B. hyalinum Lauder	2	0	—	—	—	—	—	—	—	—	—	—
B. varians Lauder	1	0	2	0	2	1	—	—	—	—	—	—
Rhizosolenia alata Brightwell	23	6	22	5	5	0	2	0	—	—	—	—
R. cylindrus Cleve	—	—	1	0	—	—	1	0	—	—	—	—
R. fragilissima Bergon	1	0	—	—	—	—	—	—	—	—	—	—
R. hebetata (Bailey) Gran	26	12	18	7	—	—	3	0	—	—	—	—
R. imbricata Brightwell	7	1	13	2	1	0	3	0	—	—	—	—
R. robusta Norman ex Pritchard	3	0	—	—	—	—	—	—	—	—	—	—
R. setigera Brightwell	—	—	10	3	1	0	2	0	1	0	—	—
R. simplex Karsten	8	2	8	0	—	—	1	0	—	—	—	—
R. stolterfothii H. Peragallo	2	0	1	0	3	0	—	—	—	—	—	—
R. tyliformis Brightwell	7	0	17	11	2	0	3	2	—	—	—	—
Guinardia blavyana H. Peragallo	—	—	—	—	3	0	—	—	—	—	—	—
Guinardia sp. non det.	1	0	—	—	—	—	—	—	—	—	—	—
Leptocylindris danicus Cleve	5	2	2	0	—	—	—	—	—	—	—	—
Dactyliosolen mediterraneus H. Peragallo	7	1	10	6	—	—	2	2	—	—	—	—
Corethron criophilum Castracane	5	0	17	0	1	0	3	0	—	—	—	—
Fragilaria granulata Karsten	1	1	14	5	1	0	—	—	—	—	—	—
F. karsteni (Karsten) Boden	5	3	9	7	—	—	1	0	—	—	1	1
Asterionella japonica Cleve & Möller ex Gran	17	9	14	7	2	0	2	1	3	3	1	1
Thalassiothrix frauenfeldii (Grün.) Cleve & Grün.	—	—	—	—	—	—	1	0	—	—	—	—
T. longissima Cleve ex Grünow	22	6	29	10	2	0	2	0	—	—	—	—
Thalassionema nitzschioides (Grün.) Hustedt	1	0	7	1	5	2	1	0	—	—	—	—
Striatella sp. non det.	—	—	1	0	—	—	—	—	—	—	—	—
Achnanthes longipes Agardh	—	—	1	0	—	—	—	—	—	—	—	—
Navicula membranacea Cleve	—	—	1	0	—	—	—	—	—	—	—	—
Navicula spp. non det.	3	0	5	0	—	—	1	0	3	0	—	—
Pleurosigma capense Karsten	3	1	1	0	—	—	—	—	—	—	—	—
Pleurosigma sp. non det.	3	0	—	—	—	—	—	—	—	—	—	—
Nitzschia closterium (Ehrb.) Wm. Smith	10	2	6	0	1	0	—	—	—	—	1	0
N. delicatissima Cleve	19	14	21	9	2	1	3	0	3	0	—	—
N. longissima (Breb.) Ralfs	2	0	6	1	—	—	—	—	—	—	—	—
N. seriata Cleve	22	9	28	18	5	4	3	3	—	—	1	0

Table 12 (*cont.*)

Species or category	First survey 39 stations		Second survey 39 stations (repeated)		Six extra stations to south of main area		Three extra stations to north of main area		Four discoloured water-samples		Station WS 1076 (extra, no counterpart on first survey)	
	Present	Dominant	Present	Dominant	Present	Dominant	Present	Dominant	Present	>5%	Present	Dominant
DINOPHYCEAE												
Prorocentrum micans Ehrenberg	—	—	—	—	—	—	—	—	3	1	—	—
Prorocentrum sp. non det.	—	—	1	0	—	—	—	—	—	—	—	—
Palaeophalacroma verrucosum Schiller	1	0	—	—	—	—	—	—	—	—	—	—
Phalacroma Rudgei Murray & Whitting	1	0	—	—	—	—	—	—	—	—	—	—
P. argus Stein	—	—	1	0	—	—	—	—	—	—	—	—
P. minutum Cleve	1	0	—	—	1	0	—	—	—	—	—	—
Phalacroma spp. non det.	—	—	1	0	—	—	—	—	—	—	—	—
Dinophysis ovum Schütt	2	0	—	—	—	—	—	—	—	—	—	—
D. sphaerica Stein	—	—	—	—	1	0	—	—	—	—	—	—
D. acuminata Claparède & Lachmann	—	—	1	0	—	—	—	—	—	—	—	—
D. schröderi Pavillard	6	0	—	—	—	—	—	—	—	—	—	—
D. schüetii Murray & Whitting	1	0	—	—	—	—	—	—	—	—	—	—
D. tripos Gourret	4	0	6	0	6	4	—	—	—	—	—	—
Gymnodinium spp. non det.	3	0	1	0	—	—	—	—	1	0	—	—
Noctiluca miliaris Suriray	1	0	2	0	5	1	—	—	—	—	—	—
Warnowia sp. non det.	—	—	1	0	—	—	—	—	—	—	—	—
Blastodinium mangini Chatton	1	0	—	—	—	—	—	—	—	—	—	—
Blastodiniacea non det.	—	—	—	—	2	0	—	—	1	0	—	—
Ellopsidaceae non det.	—	—	1	0	—	—	—	—	—	—	—	—
Sphaerodinium sp. non det.	—	—	1	0	—	—	—	—	—	—	—	—
Peridinium triquetrum (Ehrb.) Lebour	—	—	—	—	—	—	—	—	3	3	—	—
P. crassipes Kofoid	3	1	—	—	—	—	—	—	—	—	—	—
P. depressum Bailey	1	0	—	—	—	—	—	—	—	—	—	—
P. elegans Cleve	2	0	—	—	—	—	—	—	—	—	—	—
P. oceanicum Vanhöffen	8	0	—	—	—	—	—	—	—	—	—	—
Peridinium spp. non det.	36	8	39	16	6	1	2	1	3	0	1	0
Goniaulax spinifera Clap. & Lachmann	14	6	2	0	—	—	—	—	—	—	—	—
Goniaulax sp. non det.	—	—	1	0	—	—	—	—	—	—	—	—
Pyrodinium sp. non det.	1	0	—	—	—	—	—	—	—	—	—	—
Amphidoma nucula Stein	1	0	—	—	—	—	—	—	—	—	—	—
Ceratium candelabrum (Ehrb.) Stein	13	1	4	0	3	0	—	—	—	—	—	—
C. furca (Ehrb.) Clap. & Lach.	11	0	10	0	6	0	—	—	—	—	—	—
C. pentagonum Gourret	—	—	4	0	—	—	—	—	—	—	—	—
C. lineatum (Ehrb.) Cleve	11	1	4	0	2	0	—	—	—	—	—	—
C. fusus (Ehrb.) Dujardin	24	2	19	0	5	0	2	0	—	—	—	—
C. tripos (O. F. Müller) Nitzsch	9	1	6	0	6	3	—	—	—	—	—	—
C. arietinum Cleve	19	1	12	0	1	0	2	0	—	—	—	—
C. limulus Gourret	—	—	7	0	—	—	—	—	—	—	—	—
C. platycorne von Daday	4	0	—	—	—	—	—	—	—	—	—	—
C. ranipes Cleve	—	—	—	—	1	0	—	—	—	—	—	—
C. vultur Cleve	—	—	—	—	4	0	—	—	—	—	—	—
C. buceros Zacharias	—	—	1	0	—	—	—	—	—	—	—	—
C. massiliense (Gourret) Jörgensen	—	—	6	0	5	0	1	0	—	—	—	—
C. macroceros (Ehrb.) Cleve	10	0	2	0	—	—	—	—	—	—	—	—
C. trichoceros (Ehrb.) Kofoid	1	0	3	0	—	—	—	—	—	—	—	—
Goniodoma polyedricum (Pouchet) Jörg.	2	0	—	—	—	—	1	0	—	—	—	—
Goniodoma sp. non det.	1	0	—	—	1	0	—	—	—	—	—	—
Small Dinophyceae non det.	—	—	—	—	—	—	—	—	2	0	—	—
OTHER PROTOPHYTA												
Trichodesmium thiebautii Gomont [filaments]	4	1	8	3	—	—	—	—	—	—	—	—
Phaeocystis sp. non det. [colonies]	—	—	—	—	1	0	—	—	—	—	—	—
Trochischia brachiolata (Möb.) Lemm.	—	—	1	0	—	—	—	—	—	—	—	—
T. multispinosa (Möb.) Lemm.	2	0	5	0	—	—	—	—	—	—	—	—
Halosphaera viridis Schmitz	2	0	—	—	—	—	—	—	—	—	—	—
Umbilicosphaera sp. non det.	—	—	1	0	—	—	—	—	—	—	—	—
Coccosphaeriales (other) non det.	4	0	11	0	2	0	—	—	—	—	—	—
Dictyocha fibula Ehrenberg	4	0	—	—	1	0	—	—	—	—	—	—
Distephanus speculum (Ehrb.) Haeckel	1	0	2	0	—	—	—	—	—	—	—	—
PROTOZOA												
Challengeridae	7	0	16	0	4	0	—	—	—	—	1	0
Acanthometridae	4	4	5	0	—	—	—	—	—	—	—	—
Radiolaria (other)	22	1	21	0	4	0	—	—	—	—	—	—
Foraminifera	24	3	33	7	4	0	2	0	—	—	—	—
Sticholonche sp. non det.	3	0	9	0	4	0	2	0	—	—	—	—
? *Cyclotrichium meunieri* Powers	—	—	—	—	—	—	—	—	1	1	—	—

Table 12 (*cont.*)

Species or category	*First survey 39 stations* Present	Dominant	*Second survey 39 stations (repeated)* Present	Dominant	*Six extra stations to south of main area* Present	Dominant	*Three extra stations to north of main area* Present	Dominant	*Four discoloured water-samples* Present	>5	*Station WS 1076 (extra, no counterpart on first survey)* Present	Dominant
PROTOZA												
Ciliata (other, Tintinnids excepted)	—	—	4	0	—	—	—	—	—	—	—	—
Tintinnopsis spp.	4	0	2	0	1	0	—	—	—	—	—	—
Codonella spp.	1	0	17	1	—	—	2	0	—	—	—	—
Codonellopsis spp.	1	0	2	0	—	—	—	—	—	—	—	—
Favella spp.	—	—	1	0	—	—	—	—	—	—	—	—
Parafavella spp.	—	—	1	0	—	—	1	0	—	—	—	—
Epiplocylis spp.	10	0	11	0	—	—	—	—	—	—	—	—
Rhabdonella brandti Kofoid & Campbell	9	2	1	0	—	—	—	—	—	—	—	—
Rhabdonella spp.	10	1	4	0	—	—	—	—	—	—	—	—
Rhabdonellopsis spp.	2	0	1	0	—	—	—	—	—	—	—	—
Parundella spp.	—	—	3	0	—	—	—	—	—	—	—	—
Xystonella spp.	—	—	2	0	—	—	—	—	—	—	—	—
Xystonellopsis spp.	2	0	7	0	—	—	1	0	—	—	1	0
Undella spp.	6	0	7	0	—	—	—	—	—	—	—	—
Undellopsis tricollaria (Laackmann) K. & C.	1	0	—	—	—	—	—	—	—	—	—	—
Proplectella spp.	—	—	5	0	—	—	—	—	—	—	—	—
Dictyocysta spp.	20	2	13	0	—	—	2	0	—	—	—	—
Bursaopsis spp.	2	0	—	—	—	—	—	—	—	—	—	—
Amphorella spp.	2	0	2	0	—	—	—	—	—	—	—	—
Steenstrupiella spp.	—	—	—	—	—	—	2	0	—	—	—	—
Amphorellopsis spp.	—	—	1	0	—	—	—	—	—	—	—	—
Dadayiella spp.	—	—	6	0	—	—	1	0	—	—	—	—
Tintinnus lusus-undae Entz, Snr.	4	0	7	0	3	0	—	—	—	—	—	—
Salpingella spp.	2	0	1	0	—	—	—	—	—	—	—	—
Tintinnoinea (non det.)	10	0	1	0	3	0	—	—	2	0	—	—
METAZOA												
Diphyids (Siphonophora)	—	—	—	—	1	0	—	—	—	—	—	—
Chaetognatha	3	0	—	—	2	0	—	—	—	—	—	—
Polychaeta mainly larvae and post-larval	1	0	1	0	2	0	—	—	—	—	—	—
Ova: ? molluscan	2	1	—	—	—	—	—	—	—	—	—	—
Pteropoda: *Limacina* juv.	4	3	6	0	—	—	—	—	—	—	—	—
Pteropoda: ? Gymnosomata juv.	3	0	2	0	—	—	—	—	—	—	—	—
Post-larval lamellibranchs	—	—	1	0	3	0	—	—	—	—	—	—
Molluscan larvae, other	1	0	—	—	—	—	—	—	—	—	—	—
Ova: mainly Copepodan	21	10	28	3	3	0	1	0	1	0	—	—
Egg packets: mainly Harpacticid	22	3	16	1	3	0	2	0	—	—	—	—
Ova: Euphausian	2	1	?	0	—	—	—	—	—	—	—	—
Nauplii	37	16	37	14	6	2	2	1	—	—	—	—
Evadne nordmanni Lovén	—	—	—	—	1	0	—	—	—	—	—	—
Ostracoda	1	0	—	—	—	—	—	—	—	—	—	—
Copepoda	38	15	35	14	6	2	2	1	—	—	—	—
Cumacea	4	0	1	0	—	—	—	—	—	—	—	—
Euphausiidae: early larvae	1	0	5	0	3	0	—	—	—	—	—	—
Euphausiidae: late larvae → adult	—	—	3	0	—	—	—	—	—	—	—	—
Ophioplutei	1	0	—	—	—	—	—	—	—	—	—	—
Appendicularia	17	1	5	0	2	0	—	—	—	—	—	—
Doliolidae	2	0	—	—	2	0	—	—	—	—	—	—
Fish eggs	6	0	8	0	2	0	—	—	—	—	—	—
Fish larvae and post-larvae	6	0	8	0	2	0	—	—	—	—	—	—
SESTON												
Cast skins, etc.	9	4	32	10	6	1	3	0	1	0	—	—
Faecal pellets	15	7	27	4	4	0	1	0	—	—	1	0

From the full list, shorter series limited to the categories occurring as dominants (*a*) during both surveys, (*b*) during the first survey only, and (*c*) during the second survey only, have been abstracted in Table 13. Here the frequency data have been summarized in the form of double fractions. Thus the entry '*Stephanopyxis turris* 10/3 and 11/1' signifies that this species was present at ten out of the thirty-nine stations of the first survey and dominant at three of those ten; present at eleven of the second survey stations, but dominant at only one of them.

This table provides most of the basis for selection of the relatively more important forms, without which detailed consideration of the vast mass of data on distribution and relative abundance could not usefully be attempted. It seemed best to insert it here, following immediately upon the full list from which it has been derived, although the further consideration of individual species—distributions, etc. in which it has been utilized is deferred until after the description of main group distribution.

Tables 12 and 13 suffice to bring out one important difference between the rich diatom-flora of this typical subtropical upwelling region, and that of other sea areas where diatoms predominate, such as the antarctic zone of the southern ocean. The colder water flora and that of the Benguela current have alike been described as 'monotonous' (in a restricted sense) since the one class of algae predominates in both of them. The colder water flora, however, tends to be characterized by a more extreme monotony, in that one or two species are frequently found to predominate over all the others to a very marked degree, over wide areas and for long periods of time (Hart, 1934; Marumo, 1953). The Benguela current samples are very much more varied, as shown by the large number of species recorded as dominants on the criterion chosen here. Even if we apply the criterion used by the Japanese—least number of species needed to attain 50% of the total cell count—the diversity of the Benguela samples would be more than twice as great as that of many antarctic ones, at least five or six species being needed to attain this proportion in most of the catches. Indeed, when we consider the occasional predominance of dinoflagellates, and of *Trichodesmium* at some of the poorer stations, and the fact that such nannoplankton forms as Coccosphaeriales and small dinoflagellates would certainly bulk far more largely had it been practicable to use other sampling methods, it seems very doubtful whether this plankton should be regarded as 'monotonous', even in the restricted sense.

Table 13. *Abridged frequency data: Categories occurring as dominants at one or more of the thirty-nine repeated stations*

(*a*) *During both surveys*		(*b*) *During the first survey only*		(*c*) *During the second survey only*	
Stephanopyxis turris	10/3 and 11/1	*Eucampia zoodiacus*	11/4 and 0/0	*Skeletonema costatum*	1/0 and 3/1
Thalassiosira excentrica	14/3 and 3/1	*Chaetoceros costatum*	4/4 and 1/0	*Thalassiosira* spp. non det.	2/0 and 14/5
T. subtilis	12/2 and 14/3	*C. didymum* (resting spores)	13/6 and 3/0	*Coscinodiscus* spp. non det.	8/0 and 28/1
Planktoniella sol	19/6 and 24/9	*C. pseudocrinitum*	2/1 and 0/0	*Asteromphalus heptactis*	5/0 and 6/1
Chaetoceros affine	2/1 and 4/1	*C. subsecundum*	11/3 and 3/0	*Chaetoceros atlanticum*	0/0 and 15/5
C. compressum	17/13 and 24/9	*C. teres*	15/7 and 2/0	*C. lorenzianum*	2/0 and 14/9
C. constrictum	22/12 and 26/19	*C. van heurckii*	9/5 and 1/0	*C. peruvianum*	8/0 and 10/1
C. convolutum	17/7 and 22/5	*Chaetoceros* spp. non det.	3/2 and 0/0	*C. sociale*	1/0 and 5/3
C. curvisetum	15/11 and 18/12	*Rhizosolenia simplex*	8/2 and 8/0	*Rhizosolenia setigera*	0/0 and 10/3
C. debile	4/3 and 4/2	*Leptocylindrus danicus*	5/2 and 2/0	*R. styliformis*	7/0 and 17/11
C. decipiens	5/1 and 14/8	*Pleurosigma capense*	3/1 and 1/0	*Thalassionema nitzschioides*	1/0 and 7/1
C. difficile	8/5 and 14/2	*Nitzschia closterium*	10/2 and 6/0	*Nitzschia longissima*	2/0 and 6/1
C. didymum (vegetative phases)	12/6 and 10/2	*Peridinium crassipes*	3/1 and 0/0	*Codonella* spp.	1/0 and 17/1
C. strictum	11/7 and 10/6	*Goniaulax spinifera*	14/6 and 2/0		
C. tetras	4/1 and 2/2	*Ceratium candelabrum*	13/1 and 4/0		
Rhizosolenia alata	23/6 and 22/5	*C. lineatum*	11/1 and 4/0		
R. hebetata	26/12 and 18/7	*C. fusus*	24/2 and 19/0		
R. imbricata	7/1 and 13/2	*C. tripos*	9/1 and 6/0		
Dactyliosolen mediterraneus	7/1 and 10/6	*C. arietinum*	19/1 and 12/0		
Fragilaria granulata	1/1 and 14/5	Acanthometridae	4/4 and 5/0		
F. karsteni	5/3 and 9/7	Radiolaria (other)	22/1 and 21/0		
Asterionella japonica	17/9 and 14/7	*Rhabdonella brandtii*	9/2 and 1/0		
Nitzschia delicatissima	19/14 and 21/9	*Rhabdonella* spp.	10/1 and 4/0		
N. seriata	22/9 and 28/18	*Dictyocysta* spp.	20/2 and 13/0		
Peridinium spp. non det.	36/8 and 39/16	Ova, ? molluscan	2/1 and 0/0		
Trichodesmium thiebautii	4/1 and 8/3	Pteropoda: *Limacina* juv.	4/3 and 6/0		
Foraminifera	24/3 and 33/7	Ova: Euphausian	2/1 and 0/0		
Ova, mainly Copepodan	21/10 and 28/3	Appendicularia	17/1 and 5/0		
Egg packets, mainly Harpacticid	22/3 and 16/1				
Nauplii	37/16 and 37/14				
Copepoda	38/15 and 35/14				
Cast skins, etc.	9/4 and 32/10				
Faecal pellets	15/7 and 27/4				

Table 14. *First survey (autumn). Estimated numbers of the main groups and total microplankton.*

Station no.	Approx. distance from land in sea-miles	Settlement volumes (ml.)	Fractions examined	No. of categories	I Bacillariophyceae: Estimated totals	I Bacillariophyceae: % of IV	I Bacillariophyceae: % of VIII	II Dinophyceae: Estimated totals	II Dinophyceae: % of IV	II Dinophyceae: % of VIII	III Other plants: Estimated totals	III Other plants: % of IV	III Other plants: % of VIII	IV Phytoplankton: Σ (I+II+III): Estimated totals	IV Phytoplankton: Σ (I+II+III): % of VIII	V Protozoa: Estimated totals	V Protozoa: % of VIII	VI Metazoa: Estimated totals	VI Metazoa: % of VIII	VII Seston: Estimated totals	VII Seston: % of VIII	VIII Estimated microplankton totals
WS 964	103	7	1/724	27	73,124	68·2	36·7	34,028	31·8	17·1	—	—	—	107,152	53·8	52,852	26·6	39,096	19·6	—	—	199,100
WS 965	90	5	1/600	26	143,400	85·4	59·8	24,600	14·6	10·2	—	—	—	168,000	70·0	40,800	17·0	31,200	13·0	—	—	240,000
WS 966	77	8	1/1250	35	363,750	86·4	72·2	56,250	13·3	11·1	1,250	0·3	0·3	421,250	83·6	70,000	13·9	12,500	2·5	—	—	503,750
WS 967	61	11	1/10,000*	44	1,634,250	98·3	95·9	25,750	1·6	1·5	250	0·1	0·1	1,660,250	97·5	14,250	0·8	29,500	1·7	—	—	1,704,000
WS 968	43	10	1/750	29	22,500	28·8	16·3	55,500	71·2	40·2	—	—	—	78,000	56·5	18,750	13·6	41,250	29·9	—	—	138,000
WS 969	28	15	1/3,168	38	4,118,400	96·2	94·2	161,568	3·8	3·7	—	—	—	4,279,968	97·8	25,344	0·6	66,528	1·5	—	—	4,371,840
WS 970	12	8	1/250, 1/2,000	47	1,382,500	89·0	79·3	170,000	11·0	9·7	—	—	—	1,552,500	89·0	38,000	2·2	154,000	8·8	—	—	1,744,500
WS 971	30	9	1/2,000	29	386,000	58·2	46·5	262,000	41·8	33·1	—	—	—	648,000	79·6	60,000	7·7	100,000	12·7	—	—	808,000
WS 972	53	5	1/3,000	24	972,000	64·3	60·4	546,000	35·7	34·0	—	—	—	1,518,000	94·4	12,000	0·7	78,000	4·9	—	—	1,608,000
WS 973	72	8	1/2,000	25	1,010,000	61·8	58·8	624,000	38·2	36·1	—	—	—	1,634,000	95·1	12,000	0·7	72,000	4·2	—	—	1,718,000
WS 974	93	10	1/100	24	314,000	84·0	65·1	60,000	16·0	12·5	—	—	—	374,000	77·6	22,000	4·6	86,000	17·8	—	—	482,000
WS 975	112	6	1/2,000	24	202,000	63·5	51·8	116,000	36·5	29·3	—	—	—	318,000	81·1	62,000	15·8	12,000	3·1	—	—	392,000
WS 976	142	6	1/2,000	24	282,000	91·4	53·2	26,000	8·6	4·9	—	—	—	308,000	58·1	164,000	30·9	58,000	10·9	—	—	530,000
WS 977	106	13	1/2,000	25	212,000	83·5	46·7	40,000	15·7	8·8	2,000	0·8	0·4	254,000	55·9	112,000	24·7	88,000	19·4	—	—	454,000
WS 978	81	28	1/2,400	30	816,600	79·9	58·4	199,200	19·6	14·4	4,800	0·5	0·3	1,017,600	73·1	290,400	20·9	84,000	6·0	—	—	1,392,000
WS 979	48	45	1/8,000 1/192,000	31	98,328,000	99·9	99·8	56,000	<0·1	<0·1	8,000	<0·01	<0·01	98,392,000	99·9	16,000	<0·1	32,000	<0·1	—	—	98,440,000
WS 980	20	30	1/8,000, 1/64,000	28	45,344,000	98·9	98·2	512,000	1·1	1·1	—	—	—	45,856,000	93·3	—	—	320,000	0·7	—	—	46,176,000
WS 981	11	15	1/900, 1/21,600	31	9,987,300	98·1	97·0	196,200	1·9	1·9	—	—	—	10,183,500	98·9	25,200	0·2	86,400	0·8	—	—	10,295,100
WS 982	10	130	1/180,000	27	74,070,000	99·2	98·7	612,000	0·8	0·8	—	—	—	74,682,000	99·5	96,000	0·1	246,000	0·3	—	—	75,024,000
WS 983	31	28	1/600, 1/72,000	25	40,180,800	99·6	97·9	144,000	0·4	0·3	—	—	—	40,324,800	98·2	600	<0·1	720,000	1·8	—	—	41,045,400
WS 984	46	64	1/96,000*	25	69,432,000	99·9	99·2	54,000	0·1	0·1	—	—	—	69,486,000	99·3	120,000	0·2	240,000	0·3	96,000	0·2	69,942,000
WS 985	71	40	1/3,000, 1/3,600	25	27,477,000	99·8	99·5	42,000	0·2	0·1	—	—	—	27,519,000	99·6	18,000	0·1	69,000	0·3	6,000	<0·1	27,612,000
WS 986	90	? 10	1/300, 1/500	32	97,300	73·0	47·6	35,700	26·8	17·5	300	0·2	0·1	133,300	65·2	5,600	2·7	65,400	31·5	—	—	204,300
WS 987	59	14	1/300	18	11,400	16·2	6·6	58,800	83·8	33·9	—	—	—	70,200	40·5	6,900	4·0	62,100	35·8	34,200	19·7	173,400
WS 988	22	100	1/45,000, 1/300,000	19	270,450,000	100·0	99·9	—	—	—	—	—	—	270,450,000	99·9	—	—	360,000	0·1	—	—	270,810,000
WS 989	8	67	1/9,000, 1/216,000	31	158,508,000	99·9	99·8	135,000	0·1	<0·1	—	—	—	158,643,000	99·9	36,000	<0·1	63,000	<0·1	36,000	<0·1	158,778,000
WS 990	22	55	1/9,600	27	74,006,400	99·8	99·6	182,400	0·2	0·2	—	—	—	74,188,800	99·8	38,400	<0·1	57,600	0·1	38,400	<0·1	74,323,200
WS 991	38	185	1/450,000	13	258,300,000	100·0	99·8	—	—	—	—	—	—	258,300,000	99·8	—	—	450,000	0·2	—	—	258,750,000
WS 992	52	30	1/1,200, 1/96,000	33	50,692,800	99·1	98·8	268,800	0·5	0·5	192,000	0·4	0·3	51,153,600	99·6	31,200	0·1	57,600	0·1	86,400	0·2	51,328,800
WS 993	66	9	1/300	40	19,800	68·0	28·3	6,600	22·7	9·4	2,700	9·3	3·9	29,100	41·6	3,300	4·7	33,300	47·7	4,200	6·0	69,900
WS 994	87	8	1/300	35	16,800	69·1	21·1	5,400	22·2	6·8	2,100	8·7	2·6	24,300	30·5	2,100	2·6	40,200	50·4	13,200	16·5	79,800
WS 995	100	6	1/300	29	12,300	58·6	13·4	8,100	38·6	8·9	600	2·8	0·7	21,000	23·0	7,500	8·2	56,100	61·3	6,900	7·5	91,500
WS 996	130	4	1/200	33	16,000	70·8	29·5	3,200	14·2	5·9	3,400	15·0	6·3	22,600	41·7	4,000	7·5	24,800	45·7	2,800	5·1	54,200
WS 997	97	6	1/300	29	13,800	82·1	27·7	900	5·4	1·8	2,100	12·5	4·3	16,800	33·8	3,000	6·0	23,700	47·5	6,300	12·7	49,800
WS 998	78	4	1/250	16	3,000	85·7	13·3	500	14·3	2·2	—	—	—	3,500	15·5	1,000	4·5	12,250	54·5	5,750	25·4	22,500
WS 999	59	4	1/200	16	1,200	50·0	3·3	1,200	50·0	3·3	—	—	—	2,400	6·6	3,000	8·2	16,800	45·9	14,400	39·3	36,600
WS 1000	37	6	1/300	13	42,300	95·9	49·0	1,800	4·1	2·0	—	—	—	44,100	51·0	7,200	8·3	20,100	23·4	15,000	17·3	86,400
WS 1001	20	50	1/18,000	13	7,758,000	99·5	98·1	36,000	0·5	0·5	—	—	—	7,794,000	98·6	—	—	72,000	0·9	36,000	0·5	7,902,000
WS 1002	8	110	1/36,000, 1/62,000	10	43,710,000	99·6	99·6	108,000	0·4	0·3	—	—	—	43,818,000	99·9	—	—	72,000	0·1	—	—	43,890,000

* And larger fractions for the larger organisms.

Distribution of the main groups of microplankton

First survey

The estimated numbers of the main groups of microplankton present in the hauls from each station are given in Table 14, with the approximate distances of the stations from the nearest point on the coast. The fractions examined, number of species or other categories recognized in each count, and the settlement volumes of the catches are also given, together with percentages of the main groups relative to the totals, as shown by the column headings. These data, excepting the percentages, are also shown graphically in Figs. 58–64, designed to aid general description of the results on each separate line of stations.

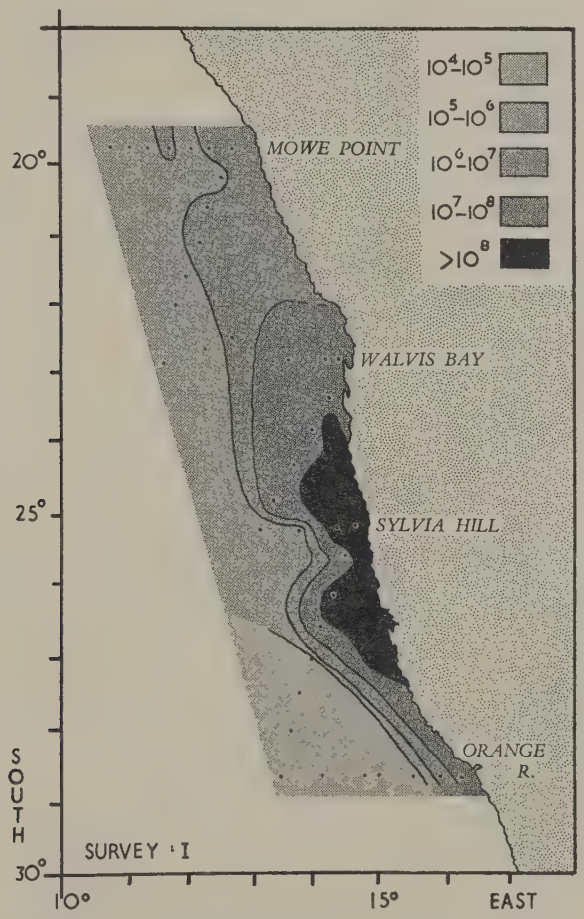

Fig. 57. Distribution of the microplankton, estimated totals per net haul, survey I, March 1950. (Station numbers are shown in Fig. 1.)

Fig. 57 shows the estimated microplankton totals in the first survey contoured logarithmically. From this the concentration of the heaviest catches in the coastal waters, more particularly in the centre of the region, is quite clear. The zone of rich coastal microplankton was narrow in the south, off the mouth of the Orange river, and reached its greatest extent seawards off Walvis Bay. The increase in width of the zone with decreasing latitude up to this point was interrupted by one deep constriction at the seaward end of the Sylvia Hill line. North of Walvis Bay the coastal microplankton was much less abundant, though still richer, especially in phytoplankton, than that of the offshore waters. The

coastal zone also narrowed again to the north, and off Möwe Point the general tendency of diminishing quantity of microplankton with increasing distance from land was somewhat obscured by the presence of relatively poor isolated catches within the coastal region. The hydrological data and qualitative plankton observations combine to show that these were due to actual tongue-like intrusions or isolated patches of more oceanic surface-water (see pp. 157, 246), with inherently poorer plankton content, and not merely to local impoverishment of the coastal water population. It would seem that the Möwe Point line was near the northern limit of the main region of upwelling at the time of this survey, and that some inter-digitation of the distinctive types of surface-water (and even some overlapping of these in the vertical plane) was the result. Such effects, well known to occur on a large scale near the

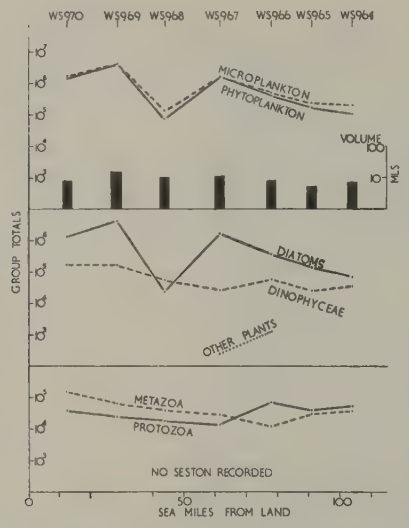

Fig. 58. Distribution of main groups of microplankton, estimated totals per net haul. Möwe Point line, survey I, 4–5 March 1950. The histogram shows the settled volumes of the catch in millimetres.

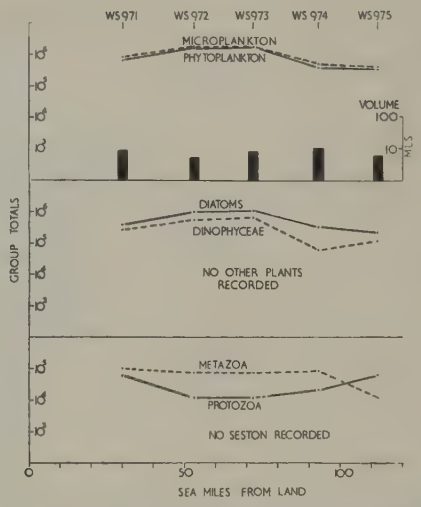

Fig. 59. Distribution of main groups of microplankton, estimated totals per net haul, survey I, Northern Intermediate line, 5 March 1950.

northern limits of the analogous Peru coastal current, must necessarily affect any simplified presentation of data collected with an arbitrarily chosen spatial limit, and plotted on the horizontal plane only, as here.

Inshore on the Sylvia Hill line the two innermost stations show, as did the stations inshore on the Walvis Bay and mid-intermediate lines, the heaviest concentrations of phytoplankton. According to the hydrological evidence (p. 162) these occur in old and rather mixed upwelled water. The two outermost stations on the Sylvia Hill line present a strong contrast. The phytoplankton, in quantity more characteristic of oceanic water, consisted of a rather neutral mixture of coastal and oceanic species. The hydrological evidence we have seen tends to link these two stations with more purely coastal water farther to the south, but the relatively high salinities and the salinity section (Fig. 15) in particular, suggest that they may lie in rather mixed oceanic water, into which some very recent upwelling was introducing a pattern of vertical layering.

One other distributional feature well shown in Fig. 57—the extreme poverty of the microplankton offshore in the south of the area, even at moderate distances from land—is much more difficult to understand. The point is reconsidered later when the results from the Orange river line are described in detail.

From Fig. 58 it can be seen that, on the Möwe Point line, the quantities of all main groups excepting Protozoa were highest inshore, with a pronounced falling off at the third station seawards, some slight secondary increase farther out and then a general decrease, most marked among the diatoms, to the low oceanic values at the seaward end of the line. 'Other plants' were observed in very small numbers some distance offshore, but not at the two outermost stations. The proportion of Dinophyceae to diatoms was above the average for the whole survey area, and Seston was not noted at the dilutions necessary to obtain counts. The relative abundance of Protozoa here was due mainly to large Radiolaria and especially tintinnids. The total estimated numbers of microplankton were relatively small throughout.

It should be noted that the stations have been plotted so that the distance scale from the land seawards reads from the left of the page, regardless of chronological sequence. This has been done so as to secure uniformity of treatment throughout the series of diagrams (Figs. 58–64, 66–72).

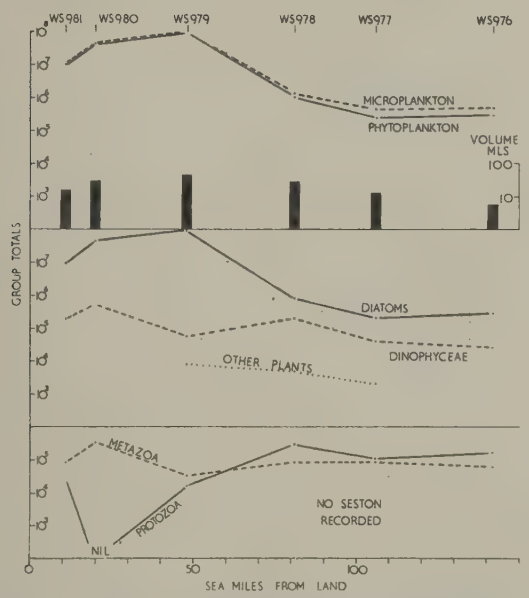

Fig. 60. Distribution of the main groups of microplankton, estimated totals per net haul, survey I, Walvis Bay line, 6–8 March 1950.

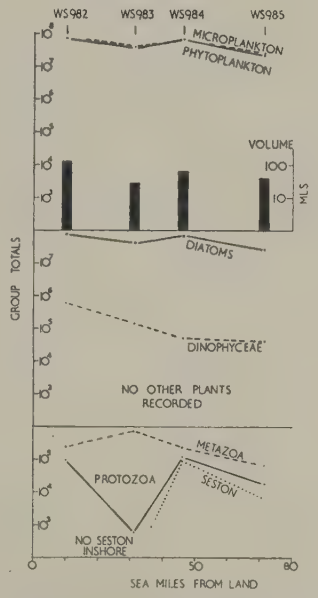

Fig. 61. Distribution of the main groups of microplankton, estimated totals per net haul, survey I, Middle–Intermediate line, 9–10 March 1950.

On the northern intermediate line the quantities of microplankton were still small and rather uniform, greatest at a moderate distance out towards the shelf-edge and least, owing mainly to the usual drop in diatom numbers, at the station farthest offshore. The proportion of Dinophyceae to diatoms was unusually high, and it will be shown later that local abundance of *Goniaulax spinifera* was mainly responsible for this. Neither 'other plants' nor Seston were observed on this line.

Conditions more typical of the Benguela current proper were first encountered on the Walvis Bay line (Fig. 60). Here the vastly greater quantities of diatoms in the inshore waters and their abrupt decrease seawards are even reflected in the settlement volumes. (The latter are rarely a reliable guide to plankton quantities, being frequently distorted by differential packing among organisms of diverse shapes, the presence of small numbers of extra large organisms, and the necessity of settling out large samples in relatively wide cylinders, so that the volumes cannot be read with the same accuracy as the small ones.) They are included only for their value as a basis for crude comparison with earlier collections in other areas, from some of which numerical estimates are not yet available.

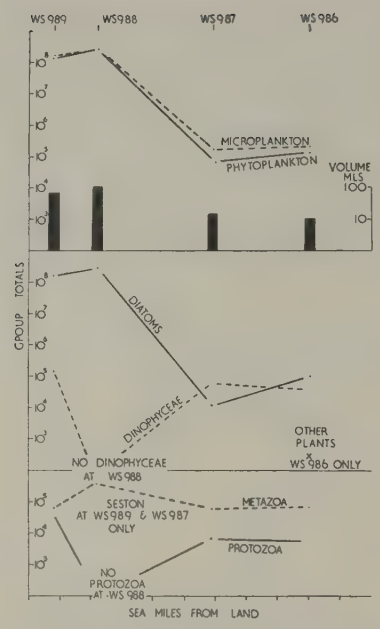

Fig. 62. Distribution of the main groups of microplankton, estimated totals per net haul, survey I, Sylvia Hill line, 10-11 March 1950.

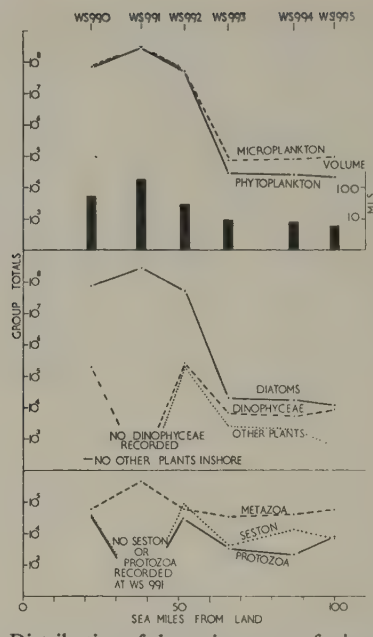

Fig. 63. Distribution of the main groups of microplankton, estimated totals per net haul, survey I, Southern Intermediate line, 11–12 March 1950.

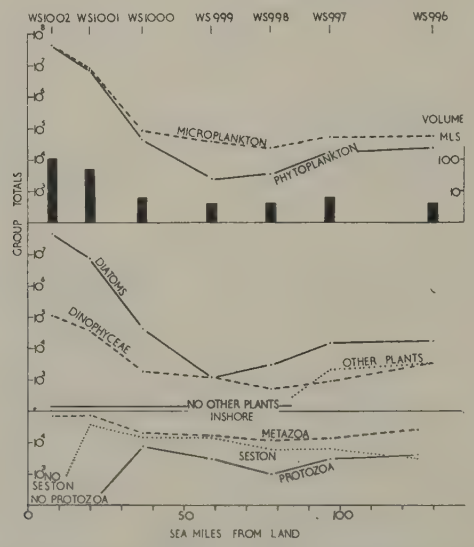

Fig. 64. Distribution of the main groups of microplankton, estimated totals per net haul, survey I, Orange river line, 12–14 March 1950.

On the Walvis Bay line Protozoa and Metazoa were present only in very moderate numbers, their *relative* importance greatly increasing beyond the point where the rich diatom plankton declined. Yet again this transition zone was the only point where 'other plants' were noted.

Rich inshore conditions persisted right out to the seaward end of the short mid-intermediate line, with large volumes, very large numbers of diatoms, and relatively few Dinophyceae (Fig. 61).

Seston was recorded at the two outer stations, the first time it had been observed (in the very small fractions used to obtain microplankton counts) during this first survey.

The Sylvia Hill line (Fig. 62) showed extreme contrast between the two diatom-rich inshore stations, and the impoverished offshore stations, where Dinophyceae were almost as numerous as the diatoms.

Again, the southern intermediate line (Fig. 63) showed very similar conditions; a heavy diatom-rich microplankton inshore; while offshore, though all the other groups showed some slight falling off in numbers from the third station seaward (where diatoms still predominated) the relative importance of those other groups was much greater in the smaller catches.

Finally, on the Orange river line (Fig. 64) the rich diatom plankton of the two inshore stations contrasted strongly with extremely small quantities of phytoplankton offshore, though moderate numbers of Protozoa, Metazoa and considerable quantities of Seston were recorded there. The capture of large numbers of herbivorous zooplankton especially the Pteropod *Limacina bulimoides* at these offshore stations, and the large quantity of Seston present, suggested that recent intensive grazing may have reduced a richer phytoplankton offshore not long before the stations were worked; because the greater width of the continental shelf at this point would lead one to expect greater seaward extension of the rich inshore conditions here at most times. The zooplankton data derive from the sorting of material from nets of coarser mesh, so that this point cannot be indicated in the uniform series of diagrams.

Second survey

Primary data concerning groups totals, relative percentages, etc., for the microplankton samples obtained during the second survey are given in Table 15. This has been constructed so that the sequence of stations, and of the lines of stations, follows that of the corresponding observations made during the first survey, regardless of their chronological order (cf. Table 14).

The total microplankton estimates for the second survey, contoured logarithmically in Fig. 65 (corresponding to Fig. 57 for the first survey) show an underlying similarity of distribution, consistent with the idea that upwelling activity proceeds (doubtless with minor fluctuations in intensity) throughout most of the year, over the major part of the area. Except in the extreme south, where the observations on the Orange river line are anomalous, rich catches inshore with rapid decrease in quantity as one proceeded seawards was the general rule. The heaviest catches of all were again obtained off Sylvia Hill and Luderitz Bay, and yet again an incursion of offshore water with contrastingly poor plankton was evident immediately seawards of the richest area, suggesting recurrence of the swirl centred (perhaps) to the south of the one encountered here during the first survey. A tongue-like intrusion of sparsely populated oceanic water in the north, on the Möwe Point line, was even more clearly defined than during the first survey, owing to the working of three extra stations to the north of the repeated series.

With all these points of resemblance to the distribution observed during the first survey there are still some differences, showing that even within a current-system apparently so persistent throughout most of the year, some seasonal changes affect the plankton population. Thus during the second survey the region of rich coastal plankton was smaller and did not extend so far seaward, especially off Walvis Bay. Conversely, the offshore microplankton, though still much more scanty than that to be found inshore, was generally somewhat richer than it had been during the first survey, especially to the north. Indeed, on the Möwe Point line (Fig. 66) only the station farthest inshore was appreciably richer in diatoms than those near the seaward end of the line. 'Other plants' were recorded only near the apparent transition point between the rapidly dwindling coastal plankton and the seasonally

Table 15. *Second survey (spring). Estimated numbers of the main groups and total microplankton*

Station no.	Approx. distance from land in sea-miles	Settlement volumes (ml.)	Fractions examined	No. of categories	I Bacillariophyceae			II Dinophyceae			III Other plants			IV Phytoplankton: Σ (I+II+III)		V Protozoa		VI Metazoa		VII Seston		VIII Estimated microplankton totals
					Estimated totals	% of IV	% of VIII	Estimated totals	% of IV	% of VIII	Estimated totals	% of IV	% of VIII	Estimated totals	% of VIII	Estimated totals	% of VIII	Estimated totals	% of VIII	Estimated totals	% of VIII	
WS 1102	110	10	1/3,000	40	1,734,000	94·9	84·1	93,000	5·1	4·5	—	—	—	1,827,000	88·6	111,000	5·5	102,000	4·9	21,000	1·0	2,061,000
WS 1101	91	15	1/6,000	38	5,208,000	98·6	96·6	72,000	1·4	1·3	—	—	—	5,280,000	97·9	54,000	1·0	54,000	1·0	6,000	0·1	5,394,000
WS 1100	75	18	1/9,000	31	4,968,000	94·1	92·3	153,000	5·9	2·9	—	—	—	5,121,000	95·2	108,000	2·0	126,000	2·3	27,000	0·5	5,382,000
WS 1099	64	7	1/900	38	185,400	80·8	55·2	42,300	18·4	12·6	1,800	0·8	0·5	229,500	68·3	29,700	8·9	63,000	18·8	13,500	4·0	335,700
WS 1098	47	12	1/6,000	27	2,082,000	95·9	85·0	90,000	4·1	3·7	—	—	—	2,172,000	88·7	96,000	3·9	108,000	4·4	72,000	3·0	2,448,000
WS 1097	31	[illegible]	1/3,000	32	1,398,000	94·3	83·7	84,000	5·7	5·0	—	—	—	1,482,000	88·7	36,000	2·2	129,000	7·7	24,000	1·4	1,671,000
WS 1096	14	25	1/24,000	22	19,320,000	99·7	99·0	48,000	0·3	0·3	—	—	—	19,368,000	99·3	120,000	0·6	24,000	0·1	—	—	19,512,000
WS 1093	33	10	1/3,600	34	3,618,000	95·3	89·1	180,000	4·7	4·4	—	—	—	3,798,000	93·5	75,600	1·9	122,400	3·0	64,800	1·6	4,060,800
WS 1091	58	6	1/2,700	36	969,300	95·5	88·0	45,900	4·5	4·4	—	—	—	1,015,200	92·2	24,300	2·2	51,300	4·6	10,800	1·0	1,101,600
WS 1090	82	12	1/3,000	35	1,317,000	97·1	85·1	36,000	2·7	2·3	3,000	0·2	0·2	1,356,000	87·6	48,000	3·1	126,000	8·1	18,000	1·2	1,548,000
WS 1089	101	6	1/900	28	117,000	72·6	35·2	44,100	27·4	13·3	—	—	—	161,100	48·5	37,800	11·4	109,800	33·1	23,400	7·0	332,100
WS 1088	117	12	1/1,500	29	1,159,500	91·2	85·0	111,000	8·7	8·1	1,500	0·1	0·1	1,272,000	93·2	25,500	1·9	52,500	3·9	13,500	1·0	1,363,500
WS 1080	144	6	1/2,700	36	483,300	91·9	78·5	42,300	8·1	6·9	—	—	—	525,600	85·4	38,700	6·3	36,900	6·0	14,400	2·3	615,600
WS 1081	117	10	1/900	26	405,000	82·0	66·0	86,400	17·5	14·1	2,700	0·5	0·4	494,100	80·5	86,400	14·1	14,400	2·3	18,900	3·1	613,800
WS 1079	83	38	1/4,500	31	1,962,000	95·4	82·5	90,000	4·4	3·8	4,500	0·2	0·2	2,056,500	86·5	117,000	4·6	121,500	5·1	81,000	3·8	2,376,000
WS 1078	48	22	1/1,500	15	25,500	51·5	10·7	24,000	48·5	10·1	—	—	—	49,500	20·8	24,000	10·1	105,000	44·0	60,000	25·1	238,500
WS 1077	21	9	1/600	35	402,600	96·1	86·1	10,200	2·4	2·2	6,000	1·5	1·3	418,800	89·6	10,800	2·3	26,400	5·6	11,400	2·5	467,400
WS 1075	10	16	1/900	29	22,923,000	99·3	98·6	153,000	0·6	0·6	18,000	0·1	0·1	23,094,000	99·3	54,000	0·2	72,000	0·4	27,000	0·1	23,247,000
WS 1074	14	10	1/3,000	28	11,835,000	99·6	98·5	36,000	0·3	0·3	18,000	0·1	0·1	11,889,000	98·9	33,000	0·2	48,000	0·4	60,000	0·5	12,030,000
WS 1073	30	10	1/1,500	31	87,000	64·4	28·7	46,500	34·4	15·4	1,500	1·2	0·5	135,000	44·6	25,500	8·4	105,000	34·6	37,500	12·4	303,000
WS 1072	48	11	1/2,400	38	820,800	92·7	75·7	62,400	7·0	5·7	2,400	0·3	0·2	885,600	81·6	48,000	4·4	108,000	10·0	43,200	4·0	1,084,800
WS 1071	73	15	1/3,000	37	2,694,000	98·4	91·8	42,000	1·5	1·5	3,000	0·1	0·1	2,739,000	93·4	36,000	1·2	123,000	4·2	36,000	1·2	2,934,000
WS 1070	94	15	1/2,400	36	1,941,600	97·6	98·5	48,000	2·4	2·2	—	—	—	1,989,600	90·9	33,600	1·5	120,000	5·5	45,600	2·1	2,188,800
WS 1069	58	16	1/600, 1/3,000	45	840,600	64·4	57·5	112,800	11·8	7·7	1,800	0·2	0·1	955,200	65·3	92,400	6·3	366,600	25·1	47,400	3·3	1,461,600
WS 1064	26	50	1/90,000	22	67,950,000	99·2	98·8	450,000	0·7	0·7	90,000	0·1	0·1	68,490,000	99·6	—	—	90,000	0·1	180,000	0·3	68,760,000
WS 1063	10	160	1/30,000, 1/300,000	27	312,300,000	99·8	99·8	450,000	0·2	0·1	—	—	—	312,750,000	99·9	30,000	<0·1	30,000	<0·1	120,000	<0·1	312,930,000
WS 1062	22	175	1/40,000, 1/400,000	23	258,680,000	99·9	99·7	80,000	<0·1	<0·1	80,000	<0·1	<0·1	258,840,000	99·8	160,000	0·1	80,000	<0·1	80,000	<0·1	259,160,000
WS 1061	28	20	1/24,000	24	27,264,000	99·3	98·9	168,000	0·7	0·7	—	—	—	27,432,000	99·6	72,000	0·2	72,000	0·2	—	—	27,576,000
WS 1060	46	18	1/12,000	24	10,740,000	99·5	97·5	48,000	0·4	0·4	12,000	0·1	0·1	10,800,000	98·0	96,000	0·9	96,000	0·9	24,000	0·2	11,016,000
WS 1059	65	15	1/600	34	199,800	49·9	44·8	12,000	3·0	2·7	189,000	47·1	42·4	400,800	89·9	7,800	1·7	30,600	6·9	6,600	1·5	445,800
WS 1058	80	15	1/1,200	37	416,400	54·6	49·2	10,800	1·4	1·3	334,800	44·0	39·6	762,000	90·1	25,200	3·0	49,200	5·8	9,600	1·1	846,000
WS 1057	97	35	1/620	34	161,200	64·7	48·8	16,120	6·5	4·9	71,920	28·8	21·8	249,240	75·5	11,760	3·6	45,880	13·8	23,560	7·1	330,460
WS 1056	128	45	1/13,200	29	6,375,600	94·9	93·2	66,000	1·0	1·0	277,200	5·1	4·0	6,718,800	98·2	39,600	0·6	52,800	0·8	26,400	0·4	6,837,600
WS 1055	94	40	1/7,200, 1/72,000	36	28,584,000	99·2	98·6	208,800	0·7	0·7	14,400	0·1	0·1	28,807,200	99·4	64,800	0·2	122,400	0·4	—	—	28,994,400
WS 1054	68	8	1/300	13	3,900	44·8	3·9	4,800	55·2	4·7	—	—	—	8,700	8·6	11,100	11·0	69,000	68·5	12,000	11·9	100,800
WS 1053	55	2	1/150	15	1,500	38·5	9·3	2,400	61·5	14·8	—	—	—	3,900	24·1	3,600	22·2	4,650	28·7	4,050	25·0	16,200
WS 1052	35	10	1/600	16	4,800	15·7	2·5	25,800	84·3	13·6	—	—	—	30,600	16·1	13,800	7·3	130,200	68·4	15,600	8·2	190,200
WS 1051	19	12	1/600	19	67,800	27·0	15·5	183,000	73·0	41·9	—	—	—	250,800	57·4	15,600	3·6	41,400	9·5	130,200	29·5	438,000
WS 1050	8	12	1/300	27	103,500	60·4	49·4	67,500	39·4	32·3	300	0·2	0·1	171,300	81·8	2,400	1·1	24,000	11·5	11,700	5·6	209,400

enriched offshore community in the poorest sample. A tendency towards restriction of this group to the transition zone had also been apparent on several of the lines worked during the first survey.

Other main groups were very evenly distributed on the Möwe Point line during the second survey. The quantities of Metazoa were moderately high, and considerable quantities of Seston were recorded, suggesting that feeding and growth of the smaller plankton animals might be proceeding more uniformly and somewhat faster at this period than in the autumn.

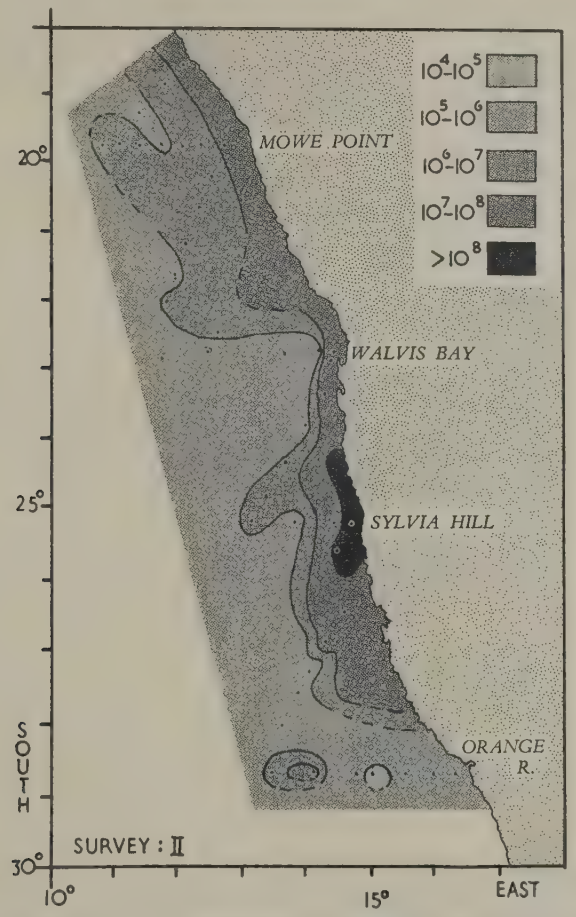

Fig. 65. Distribution of the microplankton, estimated totals per net haul, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)

On the northern intermediate line (Fig. 67) similar conditions prevailed, indicating that the relative richness of offshore phytoplankton and general abundance of small zooplankton feeding voraciously were features distinguishing the samples collected during the second survey from the ones from corresponding first survey positions.

The figures for the Walvis Bay line (Fig. 68) show a rich diatom plankton right inshore and a secondary peak at station WS 1079. The work on this line was interrupted by a gale, so that some considerable time elapsed between the working of this and the preceding inshore stations. There is hydrological evidence (p. 188) supporting the view that surface-drift of inshore water during the interval led to this apparent anomaly. In other respects the features of the microplankton distribution offshore on this line during the second survey were similar to those found farther north: moderately high

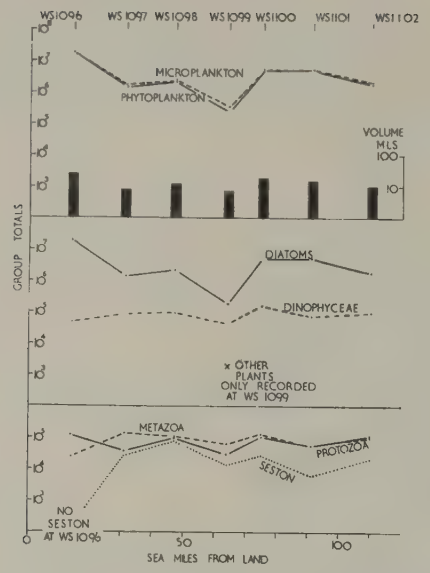

Fig. 66. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Möwe Point line, 9–11 October 1950. The histogram shows the settled volume of the catch in millimetres.

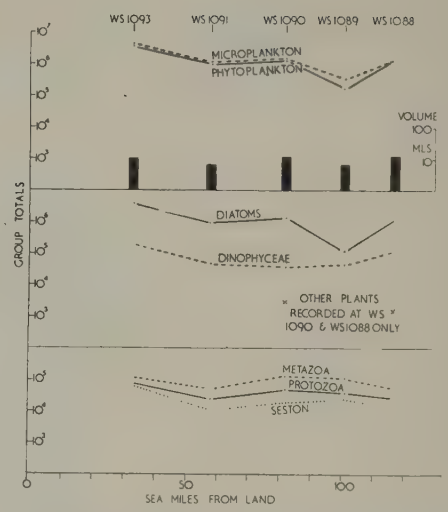

Fig. 67. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Northern Intermediate line, 8–9 October 1950.

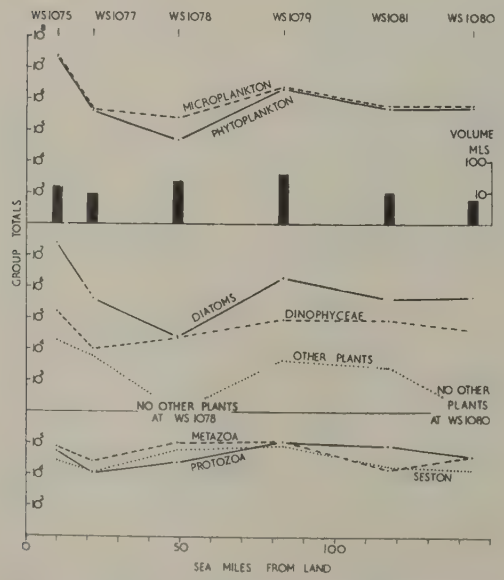

Fig. 68. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Walvis Bay line, 29 September–2 October 1950.

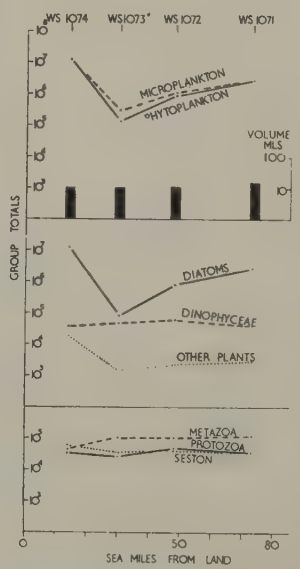

Fig. 69. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Middle Intermediate line, 28 September 1950.

values for Metazoa and Seston throughout, 'other plants' mainly in the transition zone and rather more diatoms, relatively, than had been found at the corresponding positions in autumn.

The group data for the mid-intermediate line show more profound differences from the conditions found there during the first survey. Then the diatom-rich coastal plankton had extended right out to the seaward end of the line (Figs. 61 and 65). During the second survey (Fig. 69) the rich coastal plankton with diatoms dominant was confined to the inshore station, the other groups were relatively more important throughout than they had been in autumn, and the secondary increase in diatoms towards the seaward end of the line was mainly due to offshore species. Conditions here and on the

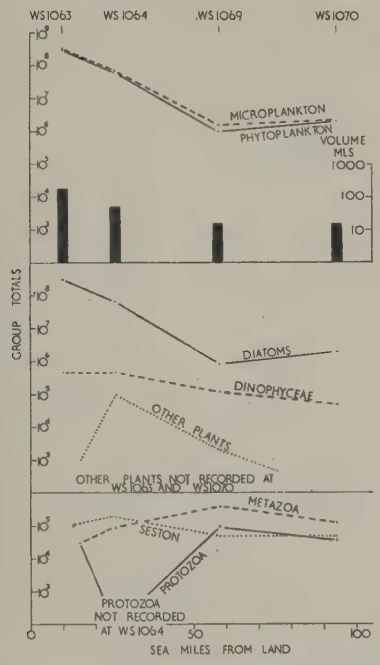

Fig. 70. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Sylvia Hill line, 21–24 September 1950.

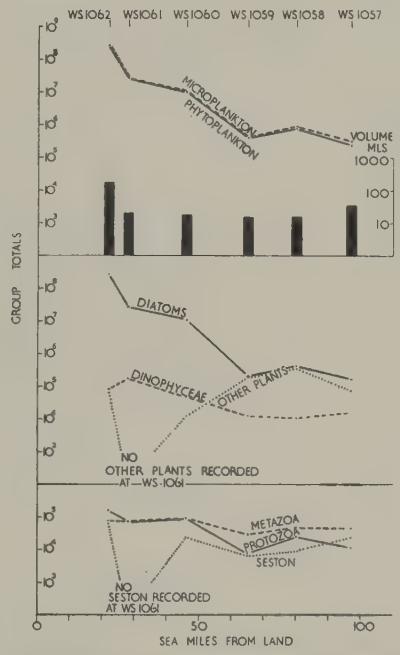

Fig. 71. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Southern Intermediate line, 24–25 September 1950.

adjacent lines both north and south displayed the general narrowing of the zone of rich coastal plankton that seemed characteristic of the second survey in its most extreme form.

The extremely rich diatom plankton found at the inshore station on the Sylvia Hill line (Fig. 70) showed clearly that, quite locally, the coastal population attained a density as great as that observed during the autumn, but proceeding seawards we again encountered the conditions met with farther north: a more rapid transition to relatively scanty offshore plankton, and greater relative abundance of Metazoa and Seston than had been observed there during the first survey.

A very similar distribution of the main groups was also evident on the southern intermediate line (Fig. 71) where the diatom population inshore was one of the richest sampled during either survey. 'Other plants', chiefly represented by isolated filaments and a few rafts of *Trichodesmium thiebautii*, attained their maximum numbers and greatest relative importance in the comparatively scanty offshore plankton on this line, but it should be emphasized that the species was not observed in anything approaching bloom-forming quantities.[1] Such blooms as we observed during the surveys were

[1] It is one of the commonest and most widely distributed bloom-forming organisms throughout the warm and temperate regions of the South Atlantic.

due to diatoms, dinoflagellates and ciliate Protozoa, but it is quite probable that *Trichodesmium* may also form blooms within the area sometimes.

The conditions observed on the Orange river line during the second survey did not conform to the generalizations found to hold good for the rest of the area (Fig. 72). Here a diatom-rich plankton with both oceanic and neritic elements was found at the two offshore stations, and inshore there was an exceptionally poor phytoplankton with a high proportion of Metazoa and Seston. The hydrological data and qualitative plankton observations give some basis for the 'explanation', necessarily somewhat speculative, of this reversal of the usual pattern of quantitative distribution that has been attempted later (p. 245).

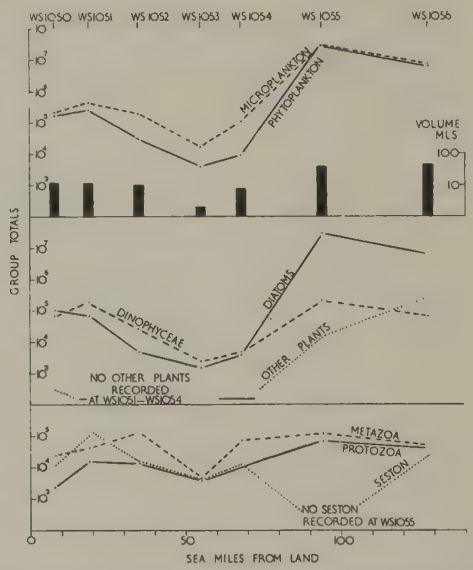

Fig. 72. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Orange river line, 21–24 September 1950.

Distribution of the main diatom groups

First survey

The distribution of the main groups of diatoms, distinguished as described on p. 214, is summarized in Table 16. This shows the estimated total diatom numbers, estimated group totals, and relative percentages for each individual station. The stations are arrayed in order of the seven lines of observations as they were worked, from north to south (cf. Table 14).

As a further aid to description, the estimated group totals have been plotted on a logarithmic scale, in relation to the distance of each station from the coast (Figs. 73–76). In these figures the distance-scale reads seawards from the left of the page for each line, departing from the chronological sequence in order to secure uniformity of treatment in this respect.

In commenting on the group distribution, reference has been made to qualitative data not given here, because the group totals alone can be misleading where they unavoidably include species of widely differing ecological attributes. This involves some repetition later, the whole difficulty resulting from the impracticability of publishing the raw data in full.

On the Möwe Point line, the estimated diatom totals were small in comparison with those for the survey as a whole. They were highest inshore and showed a secondary peak at the shelf-edge,

Table 16. *First survey (autumn). Estimated total diatoms and numbers in the main diatom groups*

Station	Estimated total diatoms	Discineae		Biddulphiineae		Chaetoceraceae		Soleniineae		'Pennatae'	
		Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
WS 964	73,124	47,060	64·4	nil	—	nil	—	19,548	26·7	6,516	8·9
WS 965	143,400	123,000	85·8	nil	—	nil	—	8,400	5·8	12,000	8·4
WS 966	363,750	26,250	7·2	nil	—	206,250	56·7	35,000	8·6	96,250	26·5
WS 967	1,634,250	61,750	3·8	30,000	1·8	1,030,000	63·0	32,500	2·0	480,000	29·4
WS 968	22,500	1,500	6·7	nil	—	2,250	10·0	12,000	53·2	6,750	30·0
WS 969	4,118,400	833,184	20·2	243,936	5·9	123,552	3·0	484,704	11·38	2,433,024	59·1
WS 970	1,382,500	108,500	7·8	112,000	8·2	172,000	12·4	810,000	58·6	180,000	13·0
WS 971	386,000	18,000	4·7	nil	—	8,000	2·1	334,000	58·6	26,000	6·7
WS 972	972,000	147,000	15·1	nil	—	33,000	3·4	231,000	23·8	516,000	57·7
WS 973	1,010,000	276,000	27·3	nil	—	nil	—	418,000	41·4	316,000	31·3
WS 974	314,000	156,000	49·7	nil	—	nil	—	46,000	14·6	112,000	35·7
WS 975	202,000	24,000	11·9	nil	—	34,000	16·8	18,000	8·9	126,000	62·4
WS 976	282,000	20,000	7·1	nil	—	6,000	2·1	58,000	20·6	198,000	70·2
WS 977	212,000	20,000	9·4	nil	—	64,000	30·2	62,000	29·3	66,000	31·1
WS 978	816,000	21,600	2·6	nil	—	552,000	67·6	74,400	9·2	68,000	20·6
WS 979	98,328,000	2,000,000	2·0	80,000	0·1	93,888,000	95·5	32,000	<0·1	2,328,000	2·4
WS 980	45,344,000	1,936,000	4·3	3,328,000	6·9	22,080,000	49·1	264,000	0·6	17,736,000	39·1
WS 981	9,987,300	2,185,200	21·9	194,400	2·0	2,570,400	25·7	69,300	0·7	4,968,000	49·7
WS 982	74,070,000	1,302,000	1·8	384,000	0·5	59,580,000	80·4	1,488,000	2·0	11,316,000	15·3
WS 983	40,180,800	2,305,200	5·7	648,000	1·6	36,792,000	91·6	72,000	0·2	363,600	0·9
WS 984	69,432,000	168,000	0·2	nil	—	67,968,000	97·9	336,000	0·5	960,000	1·4
WS 985	27,477,000	396,000	1·4	nil	—	25,992,000	94·6	45,000	0·2	1,044,000	3·8
WS 986	97,300	4,300	4·4	2,500	2·6	34,000	34·9	10,000	10·3	46,500	47·8
WS 987	11,400	3,600	31·5	nil	—	6,900	60·5	900	8·0	nil	—
WS 988	270,450,000	9,720,000	3·6	7,470,000	2·7	208,170,000	77·0	4,005,000	1·5	41,085,000	15·2
WS 989	158,508,000	8,649,000	5·5	4,329,000	2·7	118,872,000	75·0	1,512,000	0·9	25,146,000	15·9
WS 990	74,006,400	4,147,200	5·6	105,600	0·2	56,448,000	76·3	614,400	0·8	12,691,200	17·1
WS 991	258,300,000	nil	—	nil	—	243,450,000	94·3	nil	—	14,850,000	5·7
WS 992	50,692,800	100,800	0·2	96,000	0·2	45,024,000	88·8	nil	—	5,472,000	10·8
WS 993	19,800	4,200	21·2	nil	—	9,300	47·0	4,500	22·7	1,800	9·1
WS 994	16,800	1,800	10·7	nil	—	5,100	30·4	2,400	14·3	7,500	44·6
WS 995	12,300	1,800	14·6	nil	—	8,400	68·3	nil	—	2,100	17·1
WS 996	16,000	3,000	18·8	nil	—	2,000	12·5	4,000	25·0	7,000	43·7
WS 997	13,800	4,500	32·6	nil	—	300	2·2	2,400	17·4	6,600	47·8
WS 998	3,000	750	25·0	nil	—	500	16·7	nil	—	1,750	58·3
WS 999	1,200	nil	—	nil	—	200	16·7	400	33·3	600	50·3
WS 1000	42,300	300	0·7	nil	—	41,400	97·9	600	1·4	nil	—
WS 1001	7,758,000	nil	—	nil	—	7,434,000	95·8	nil	—	324,000	4·2
WS 1002	43,710,000	nil	—	nil	—	38,006,000	87·0	nil	—	5,704,000	13·0

diminishing to characteristically small oceanic values offshore. There was a marked minimum between the two peaks, believed to be due to intrusion of offshore water.

Considering the groups severally, it can be seen that the Discineae reached their greatest numbers in the richer inshore water. Here the neritic *Stephanopyxis* was dominant. The greatest relative importance of the group was attained at the poorer offshore stations, however, where the essentially oceanic *Planktoniella sol* accounted for most of the group-total.

Biddulphiineae were observed only at the two inshore stations, and at the secondary peak station near the shelf-edge. The neritic species *Eucampia zoodiacus* was the only one seen in the fractions counted, and the group was of little relative importance.

Chaetoceros species were unusually scanty close inshore, but predominated at the shelf-edge peak station. The group was not seen at all at the two offshore stations though these were re-examined carefully.

Soleniineae were abundant close inshore, present elsewhere in very moderate numbers, becoming of some relative importance only in the very small minimal haul, and again at the outer end of the line. *Leptocylindrus danicus*, one of the few neritic species in this essentially holoplanktonic group, was mainly responsible for the inshore maximum. Various *Rhizosolenia* species, among the most cosmopolitan of all plankton diatoms, were present at the minimal station; while right offshore the oceanic species *Rhizosolenia simplex* was the dominant form.

'Pennatae' formed an unusually high proportion of the total diatom count at the inshore peak station and were second only to Chaetoceros among the group totals at the shelf-edge peak. The small 'reversionary plankton forms' *Nitzschia* spp. and *Asterionella japonica* were chiefly responsible, with a considerable proportion of the larger *Thalassiothrix longissima* at the shelf-edge. The latter usually showed a more oceanic distribution than other members of the group in these surveys.

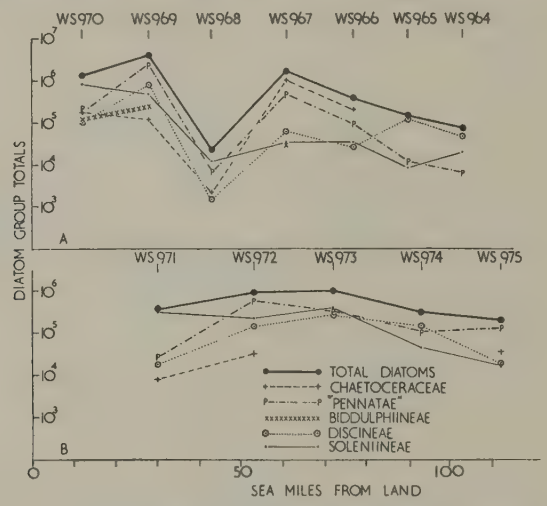

Fig. 73. Estimated total diatoms, and diatom group totals, survey I. A. Möwe Point line, 4–5 March 1950. B. Northern Intermediate line, 5 March 1950.

On the northern intermediate line, the estimated diatom totals were very moderate throughout, with a slight maximum at the second and third stations seaward, diminishing to the outer end of the line.

From the group figures it appears that Discineae were relatively somewhat more important in the small catches here than over the survey area generally. The panthalassic species *Thalassiosira excentrica* and *Planktoniella sol* (oceanic) were both among the dominants at the three slightly richer stations at the middle of the line. This may have been due to the mixing conditions thought to have obtained within the '*Goniaulax*-patch' (see p. 251).

Biddulphiineae were not observed in the routine analyses on this line and species of Chaetoceros were present in small number at the two inshore stations only. A majority of this group proved to be mainly neritic throughout the survey, but on the other lines they were nearly always dominant inshore; not the most poorly represented group, as here. Soleniineae were dominant inshore and at the peak station, represented mainly by panthalassic cosmopolitan species such as *Rhizosolenia hebetata* and *R. alata*; the falling off in relative importance of this group towards the seaward end of the line was an unusual feature thought to be bound up with the mixing conditions referred to above.

On this northern intermediate line the 'Pennatae' were the most important single group numerically, with the minute *Nitzschia delicatissima* the most important individual species, joined by the large

Thalassiothrix longissima at the seaward end of the line (one of the few details in which this series approached a norm for the area as a whole!).

On the Walvis Bay line (Fig. 74) the estimated diatom totals reached high values at the three inshore stations, with a sharp decline beyond the shelf-edge, levelling out to moderate amounts at the two oceanic offshore stations. The high inshore values proved typical of the main upwelling region on most of the lines worked throughout both surveys, as can be seen from the subsequent diagrams.

Discineae were present in fair numbers inshore, represented mainly by *Stephanopyxis turris* and *Thalassiosira subtilis*, the one definitely a neritic species, the other panthalassic. Offshore the numbers declined, at first in parallel with the estimated diatom totals, levelling at the two outer stations to give a slight secondary increase in relative importance. This was due mainly to the species *Thalassiosira*

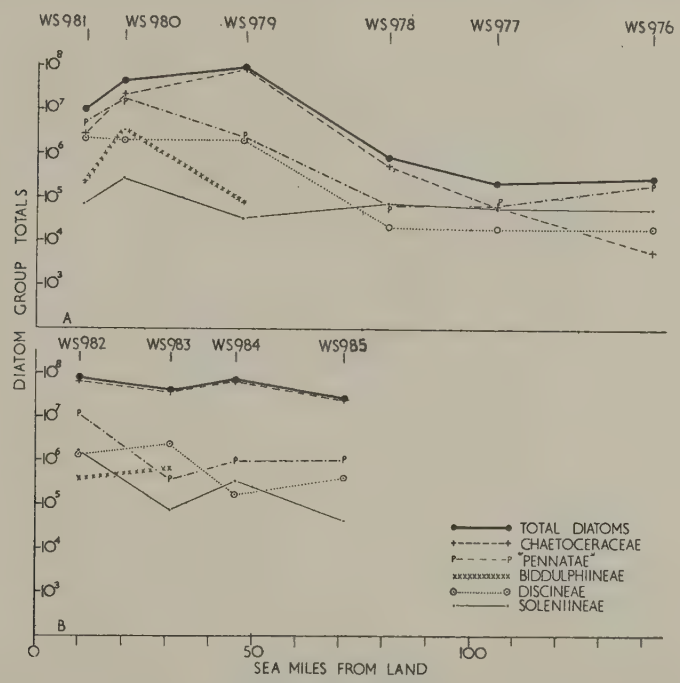

Fig. 74. Estimated total diatoms, and diatom group totals, survey I. A. Walvis Bay line, 6–8 March 1950. B. Middle Intermediate line, 9–10 March 1950.

excentrica, with lesser numbers of *Planktoniella sol*. Biddulphiineae were present inshore and of considerable importance at station WS 980, but were not observed seawards of the peak station WS 979. The group was represented here entirely by *Eucampia zoodiacus*, as on the Möwe Point line.

Chaetoceros was by far the most important group over the Walvis Bay line as a whole. It was strongly dominant at the two richest inshore stations, where a profusion of neritic species were present, and at the first of the poorer stations, seawards. There, however, the single 'relatively oceanic' species *Chaetoceros convolutum* alone accounted for most of the group total. Still further offshore the group dwindled rapidly, both in estimated numbers and in relative importance.

Soleniineae were present at all stations on the line in consistently small numbers, becoming relatively important in the poorest offshore plankton. Cosmopolitan *Rhizosolenia* spp. predominated throughout, accompanied at one inshore station, where the group total was highest, by the mainly neritic *Dactyliosolen mediterraneus*.

'Pennatae' were an important group on this line, especially at the innermost and outermost stations

where they predominated. Even at the intervening stations they ranked second only to the chaetocerids. The unavoidably heterogeneous nature of the group, however, was very evident. Whereas inshore the strongly neritic species *Fragilaria karsteni* predominated, along with *Asterionella japonica*, it was the oceanic *Thalassiothrix longissima* and panthalassic *Nitzschia delicatissima* that accounted for nearly all of the group totals farther out.

The mid-intermediate line proved too short to extend beyond the rich coastal diatom zone. The estimated diatom totals were high throughout and very closely paralleled by the group-totals for the

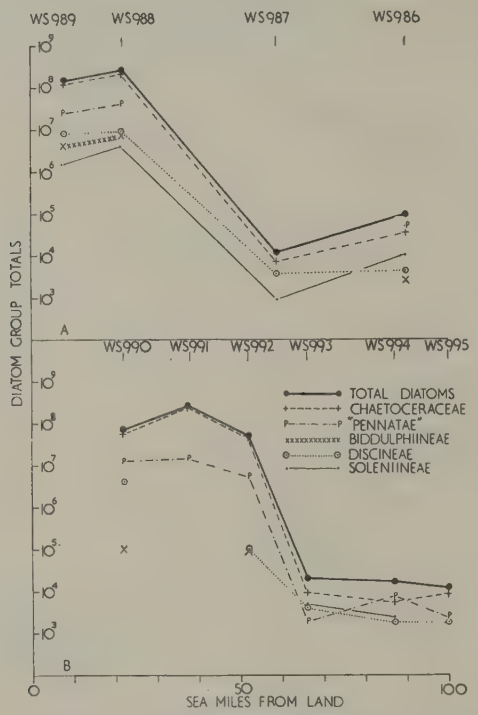

Fig. 75. Estimated total diatoms, and diatom group totals, survey I. A. Sylvia Hill line, 10–11 March 1950. B. Southern Intermediate line, 11–12 March 1950.

predominating chaetocerids. The other groups clearly fulfilled a minor role, much on the same level, with 'Pennatae' of some consequence inshore. Apart from the profusion of neritic *Chaetoceros* species, at least ten in number, the species of most importance were:

Among the Discineae, inshore, *Stephanopyxis turris* diminishing rapidly as one proceeded seawards; and *Thalassiosira subtilis*, which reached its highest numbers and relative importance at station WS 983.

Among the Biddulphiineae, *Eucampia zoodiacus* at the two inshore stations only.

Among the Soleniineae, *Dactyliosolen mediterraneus* and much lesser numbers of the more cosmopolitan *Rhizosolenia* spp. farther offshore.

Among the 'Pennatae', *Fragilaria Karsteni* and *Asterionella japonica* inshore with *Thalassiothrix longissima* at station WS 984.

On the Sylvia Hill and southern intermediate lines, diatom distribution followed an essentially similar pattern. Very high estimated totals were recorded inshore, with an abrupt decrease near the shelf-edge some 60 sea-miles from the land, and a levelling out to very low values towards the sea-

ward ends of each series of observations. Chaetocerids were by far the most important group, as can be seen from the way in which their group-totals follow closely in parallel with the figures for total diatoms. Inshore they were represented by the usual rich variety of species, mainly neritic but some with panthalassic tendencies. Offshore there was some apparent overspill of the most abundant inshore forms, but the more definitely oceanic members of the genus, such as *Chaetoceros convolutum* and *C. peruvianum*, were relatively much more important in the very poor phytoplankton met with there.

The estimated totals for other groups was also greatest inshore, but the relative importance of those with offshore representatives was much greater near the shelf-edge and beyond.

The Discineae were represented mainly by *Thalassiosira* spp. Of these *T. hyalinum*, *T. rotula* and the panthalassic *T. subtilis* were commonest inshore; *T. excentrica* and *T. subtilis* (again!) offshore. The oceanic *Planktoniella sol* was of some relative importance in one extremely small sample from near the outer end of the southern intermediate line.

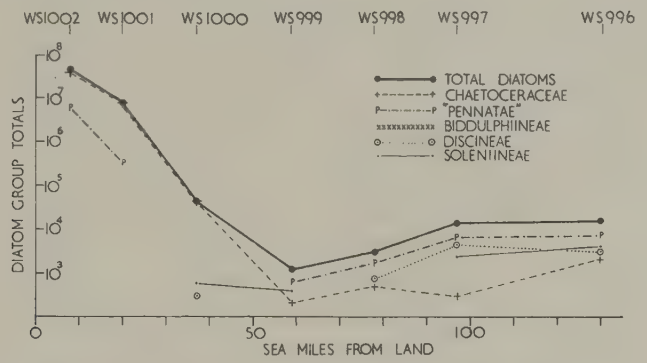

Fig. 76. Estimated total diatoms, and diatom group totals, survey I, Orange river line, 12–14 March 1950.

The Biddulphiineae were almost entirely confined to the inshore stations on both series, though *Eucampia zoodiacus* was recorded in very small numbers from station WS 986, at the seaward end of the Sylvia Hill line. This same species accounted for most of the inshore totals for the group, as we had found farther north at this season, but here there was a small proportion of *Cerataulina pelagica* in addition.

Soleniineae formed only a small proportion of these samples. The higher numbers at three inshore stations were due to the mainly neritic species *Dactyliosolen mediterraneus* and *Leptocylindrus danicus*. The very small totals for this group at offshore stations show that it was of some slight relative importance there, but only because of the prevailing poverty of the offshore phytoplankton. The offshore species included *Bacteriastrum hyalinum*, the more cosmopolitan *Rhizosolenia* spp. and *R. simplex*.

The 'Pennatae' were more heavily outnumbered by the dominant chaetocerids at the inshore stations of these two lines than they had been farther north, but still ranked second among the diatom groups. The dominant inshore species—*Fragilaria karsteni*, *Asterionella japonica* and *Nitzschia seriata*—were the same as those recorded on the two previous lines. Offshore small numbers of *Nitzschia delicatissima*, *N. seriata* and *Thalassiothrix longissima* accounted for most of the group totals, together with *Fragilaria granulata* at station WS 994. This species was recorded only at this one station during the first survey, but much more frequently and abundantly during the second, when it showed a consistently offshore distribution. The very small totals of 'Pennatae' recorded at stations WS 986 and 994 just suffice to indicate greater relative importance than that of the chaetocerids, so clearly dominant at all the other stations of the Sylvia Hill and southern intermediate lines.

Although the very great difference in quantity between the rich diatoms inshore and the impoverished phytoplankton population farther out is well shown by these two series of observations, the qualitative distinctions are less clear than they seemed to be on other lines worked during the first survey. This is believed to be due to the wide tolerance of the more panthalassic species of *Chaetoceros*, *Nitzschia* and *Thalassiosira*. Prolongation of the lines seaward would almost certainly have demonstrated their replacement as dominants by more exclusively oceanic species, but this desideratum could not be foreseen in planning the surveys. 'Ideal' coverage can never be wholly attainable in such work, and had we extended these two series, practical considerations of steaming time, fuel consumption and water supply must have enforced a corresponding curtailment of the rest of the ship's programme.

The inshore zone of rich diatom phytoplankton was narrower on the Orange river line (Fig. 76) although the shelf is wider there, and diatoms were exceptionally scanty for a considerable distance seaward. Even at the two stations right out beyond the shelf-edge the catches were still very small. Peculiar local conditions must have obtained here, for the rich zooplankton and abundance of Seston indicate heavy grazing of what must have been a very much richer standing crop of plants not long before. Further deviation from the conditions prevailing farther north were indicated by the presence of essentially neritic species along with the oceanic ones at the stations farthest from land.

Even so, apart from the narrowing of the rich coastal belt and extreme poverty of the outer stations on the shelf, the group distribution of diatoms on this line still shows *some* of the main features observed farther north. Thus most of the chaetocerids so completely dominant inshore were neritic ones, although the panthalassic species *Chaetoceros convolutum* was present in greater proportion than was usual inshore elsewhere. The decline in relative importance of this group at the impoverished offshore stations, with correspondingly increased proportions of Discineae, Soleniineae and 'Pennatae' there, is well shown in Fig. 76.

Specific data for the groups other than *Chaetoceros* show that the panthalassic *Thalassiosira subtilis* and oceanic *Planktoniella sol* among the Discineae and *Thalassiothrix longissima* among the 'Pennatae' were relatively more important offshore as in the other more normal series.

Second survey

Similar treatment of the data from the Möwe Point line on the second survey shows that at that season, although the inshore station was still the richest by far, the diatom totals diminished rapidly as the ship proceeded offshore. A minimum was reached at station WS 1099 near the edge of the shelf and there was then a considerable secondary rise in estimated totals at the three offshore stations (Table 17 and Fig. 77).

Totals for each of the four main diatom groups present[1] varied roughly in parallel with those for total diatoms, but whereas the numbers and the proportion of *Chaetoceros* and 'Pennatae' were greatest inshore, there were many more Soleniineae present at the outer stations. These outer stations were somewhat less well defined qualitatively than those on some of the more southerly series at group level, since they still contained a moderately high proportion of Discineae and *Chaetoceros*, both groups containing a majority of inshore species. The more detailed data seem to show up their distinction fairly clearly, though there was evidently more tendency towards offshore transport in the turbulent conditions prevailing than had been observed during the autumn survey.

Among the Discineae the inshore maximum was due mainly to *Stephanopyxis turris* and *Thalassiosira* spp. Though the secondary rise in numbers of the group at the offshore stations included some of these two categories, *Stephanopyxis* there formed a much smaller proportion of the totals, *Thalas-*

[1] Biddulphiineae were not observed on this line.

Table 17. *Second survey (spring). Estimated total diatoms and numbers in the main diatom groups*

Station	Estimated total diatoms	Discineae		Biddulphiineae		Chaetoceraceae		Soleniineae		'Pennatae'	
		Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
WS 1102	1,734,000	42,000	2·4	nil	—	606,000	34·9	729,000	42·1	357,000	20·6
WS 1101	5,208,000	162,000	3·1	nil	—	1,632,000	31·3	2,640,000	50·7	774,000	14·9
WS 1100	4,968,000	189,000	3·8	nil	—	792,000	15·9	3,609,000	72·7	378,000	7·6
WS 1099	185,400	9,000	4·9	nil	—	28,800	15·5	49,500	26·7	98,100	52·9
WS 1098	2,082,000	90,000	4·3	nil	—	930,000	44·7	300,000	14·4	762,000	36·6
WS 1097	1,398,000	132,000	9·4	nil	—	531,000	38·0	105,000	7·5	630,000	45·1
WS 1096	19,320,000	3,072,000	15·9	nil	—	11,064,000	57·3	936,000	4·8	4,248,000	22·0
WS 1093	3,618,400	489,600	13·5	nil	—	2,091,600	57·8	126,000	3·5	911,200	25·2
WS 1091	969,300	51,300	5·3	nil	—	221,400	22·8	518,400	53·5	178,200	18·4
WS 1090	1,317,000	81,000	6·2	nil	—	492,000	37·4	609,000	46·2	135,000	10·2
WS 1089	117,000	16,200	13·8	nil	—	9,900	8·5	85,500	73·1	5,400	4·6
WS 1088	1,159,500	1,500	0·1	nil	—	48,000	4·1	1,101,000	95·0	9,000	0·8
WS 1080	483,300	18,900	3·9	nil	—	8,100	1·7	405,000	83·8	51,300	10·6
WS 1081	405,000	10,800	2·7	nil	—	24,300	6·0	256,500	63·3	113,400	28·0
WS 1079	1,962,000	58,500	3·0	nil	—	198,000	10·1	1,206,000	61·4	499,500	25·5
WS 1078	25,500	7,500	29·4	nil	—	nil	—	nil	—	18,000	70·6
WS 1077	402,600	133,800	33·2	8,400	2·1	87,600	21·8	nil	—	172,800	42·9
WS 1075	22,923,000	576,000	2·5	nil	—	11,061,000	48·3	45,000	0·2	11,241,000	49·0
WS 1074	11,835,000	315,000	2·7	6,000	<0·1	1,326,000	11·2	6,000	<0·1	10,182,000	86·0
WS 1073	87,000	19,500	22·4	nil	—	52,500	60·3	3,000	3·5	12,000	13·8
WS 1072	820,800	79,200	9·6	nil	—	168,000	20·5	393,600	48·0	180,000	21·9
WS 1071	2,694,000	39,000	1·4	nil	—	195,000	7·2	1,698,000	63·1	762,000	28·3
WS 1070	1,941,600	52,800	2·7	nil	—	734,400	37·8	508,800	26·2	645,600	33·3
WS 1069	840,600	882,00	10·5	nil	—	654,000	77·8	22,800	2·7	75,600	9·0
WS 1064	67,950,000	630,000	0·9	270,000	0·4	64,800,000	95·4	180,000	0·3	2,070,000	3·0
WS 1063	312,300,000	1,200,000	0·4	30,000	<0·01	296,100,000	94·8	210,000	<0·1	14,760,000	4·7
WS 1062	258,680,000	1,000,000	0·4	480,000	0·2	236,800,000	91·6	nil	—	20,400,000	7·8
WS 1061	27,264,000	2,136,000	7·8	24,000	0·1	19,440,000	71·3	nil	—	5,664,000	20·8
WS 1060	10,740,000	252,000	2·3	nil	—	6,816,000	63·5	nil	—	3,672,000	34·2
WS 1059	199,800	36,000	18·0	nil	—	19,800	9·9	19,200	9·6	124,800	62·3
WS 1058	416,400	44,400	10·7	3,600	0·9	84,000	20·2	36,000	8·6	248,400	59·6
WS 1057	161,200	72,540	45·0	nil	—	14,260	8·8	11,160	7·0	63,240	39·2
WS 1056	6,375,600	171,600	2·7	39,600	0·6	4,422,000	69·4	198,000	3·1	1,544,400	24·2
WS 1055	28,584,000	1,281,600	4·5	nil	—	25,488,000	89·2	72,000	0·2	1,742,400	6·1
WS 1054	3,900	2,100	53·8	nil	—	nil	—	nil	—	1,800	46·2
WS 1053	1,500	1,050	70·0	nil	—	150	10·0	nil	—	300	20·0
WS 1052	4,800	3,000	62·5	nil	—	nil	—	nil	—	1,800	37·5
WS 1051	67,800	24,000	35·4	nil	—	38,400	56·6	600	0·9	4,800	7·1
WS 1050	103,500	39,600	38·3	nil	—	55,200	53·3	nil	—	8,700	8·4

siosira showed specific differences, and there was a very marked increase in the typically oceanic *Planktoniella sol* (absent inshore) from station WS 1099 seawards.

Some of the dominant coastal chaetocerids persisted (in reduced numbers) to the outer end of the line, but again more typically offshore forms such as *C. convolutum* and *C. lorenzianum* showed marked increase in relative importance from station WS 1099 seawards. Similar specific differences were shown within the two other groups also: Inshore *Rhizosolenia setigera* and *Leptocylindrus danicus* were the most important solenoids, while offshore *Rhizosolenia styliformis* and *Dactyliosolen mediterraneus* were the most abundant of all the diatoms at this time. *Fragilaria karsteni* and *Asterionella japonica* were among the dominant 'Pennatae' inshore. The former was not seen more than 30 sea-miles from land, and though *Asterionella* was found farther out it was present only in relatively small numbers there. The cosmopolitan *Nitzschia seriata* was observed in both localities, but offshore it appeared that *N. delicatissima* was the most numerous species of the group at this season.

The results from the northern intermediate line showed essentially the same features as those observed off Möwe Point, most of them even more definitely (Fig. 77). It is true that *Fragilaria karsteni* was not present among the 'Pennatae' at the inshore station, but this was 30 miles from the land, and from all our other observations the species seemed to be the most strongly neritic in habit of all the important plankton forms in this area. The solenoid community, with some few of the more oceanic *Chaetoceros* spp. was even more completely dominant offshore, where the line extended into a region where almost all the microplankton was essentially oceanic in character. At station WS 1088, no less than 94% of the diatoms was made up of the cosmopolitan *Rhizosolenia* spp. *R. styliformis*, *R. hebetata* and *R. imbricata*.

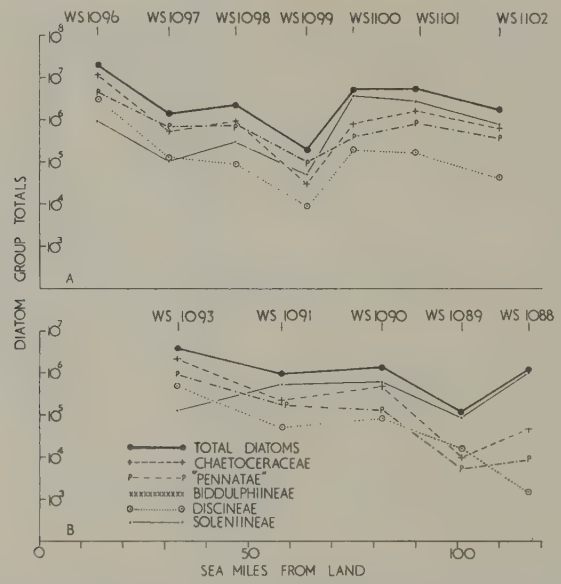

Fig. 77. Estimated total diatoms and diatom group totals, survey II. A. Möwe Point line, 9–11 October 1950. B. Northern Intermediate line, 8–9 October 1950.

The dominance of this solenoid community at offshore stations persisted in very marked degree at the outer end of the Walvis Bay line, where, however, there was a larger proportion of *Thalassiothrix longissima*, perhaps the most oceanic of the 'Pennatae', among the small fraction of the total not accounted for by the solenoids. Indeed it would appear that with minor modifications the solenoids predominated in the offshore plankton from about the middle of the area to the northern limit of our serial observations at the time of this second survey (cf. Table 17, Figs. 76–8).

The inshore stations on both the Walvis Bay and mid-intermediate lines also displayed common features that differed markedly from those observed in autumn. In spring the rich coastal flora of *Chaetoceros* spp., with *Asterionella* and *Fragilaria karsteni* among the 'Pennatae', etc., was confined to the innermost stations, with an abrupt diminution seawards *before* the shelf-edge was reached. There was thus a pronounced narrowing of the rich coastal belt here in spring, where it had been wide, and fanned out seaward to the shelf-edge on the Walvis Bay line, during the first (autumnal) survey (cf. Fig. 57 and Fig. 65). The spring results resembled more the extreme contrast within a relatively short distance out from the coast, that had been shown on the Sylvia Hill line, immediately to the southward, in autumn. The distributional pattern is consistent with the active upwelling which was demonstrated by the hydrological results from this region. Within the upwelling water, the larger

concentrations of phytoplankton were found at the stations nearest to the coast, and there was a rapid decrease seawards before even the shelf-edge was reached. On the occasions where the stations extended far enough from the coast, a secondary increase in the phytoplankton is evident—the abundance beyond the shelf-edge was greater than on the first survey. The population in this secondary increase included some oceanic forms among its dominants and it seems probable that it was associated with the divergence of oceanic water beyond the shelf-edge, which was postulated in the interpretation of the mechanism of upwelling (p. 188, Fig. 37).

Turning to conditions observed on the Sylvia Hill line itself during the second survey (Fig. 79) it can be seen that although the falling-off seawards was pronounced, diatom members were still very

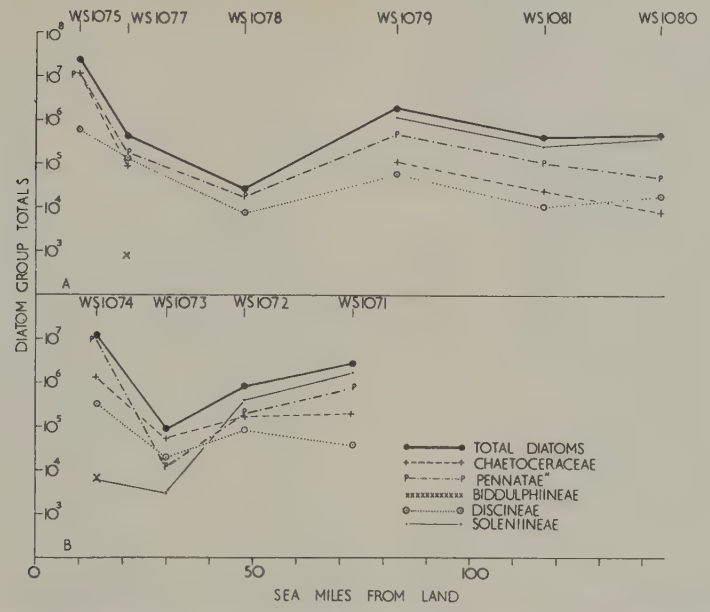

Fig. 78. Estimated total diatoms and diatom group totals, survey II. A. Walvis Bay line, 29 September–2 October 1950. B. Middle Intermediate line, 28 September 1950.

high at the second station seawards, with coastal chaetocerids and 'Pennatae' still strongly dominant. While the neritic Biddulphiineae were observed at the inshore station only, as was to be expected, members of the other two groups persisted right to the outer end of this comparatively short line, and it was only at the outermost station that the oceanic solenoids became equally important. This distribution resembled that seen on the mid-intermediate line (that next to the N. in the series) during the first survey.

On the southern intermediate line, the falling-off in quantity from the exceptionally rich inshore station was steep, but the succeeding stations seawards were still quite rich and showed a typical coastal flora extending fully 50 sea-miles from the coast. It seems probable that here again the inshore stations were characteristic of the active upwelling shown on the Sylvia Hill line. The sharp fall in abundance from station WS 1060 to station WS 1059, and the persistence at the latter station and those towards the seaward end of the line of a scanty oceanic type of plankton, was correlated with the pronounced intrusion of oceanic water to the north of the Orange river line, illustrated by the surface-temperature pattern (Fig. 7*b*).

The detailed figures for the southern intermediate line in spring show some minor anomalies at group level that require comment. At the outer oceanic station Discineae and 'Pennatae', both

groups containing a majority of inshore species, were relatively important. The individual counts show, however, that the oceanic species *Planktoniella sol* accounted for most of these Discoidae, and the typically offshore species *Thalassiothrix longissima* and *Fragilaria granulata* were prominent among the 'Pennatae', though in that group panthalassic *Nitzschia* spp. were also numerous. It was here that

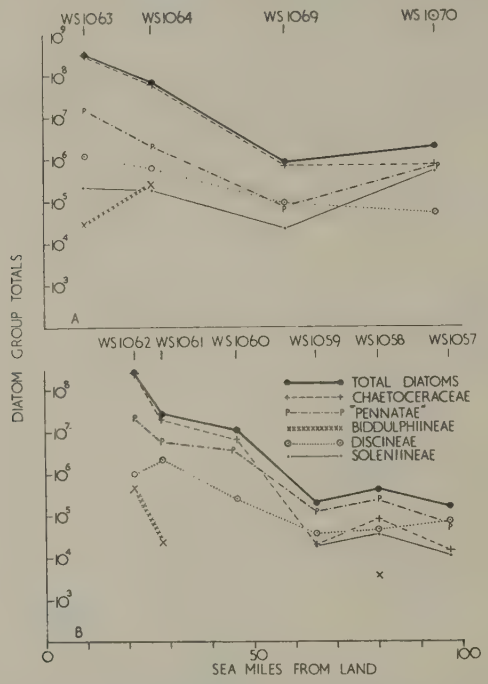

Fig. 79. Estimated total diatoms and diatom group totals, survey II. A. Sylvia Hill line, 25–27 September 1950. B. Southern Intermediate line, 24–25 September 1950.

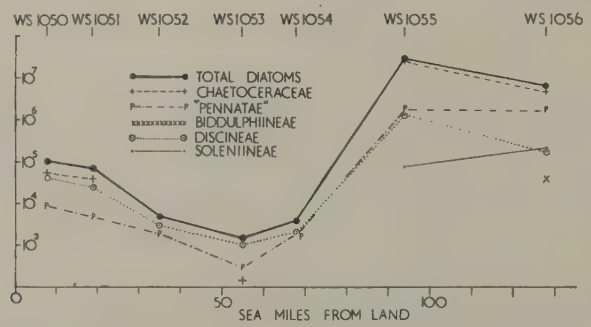

Fig. 80. Estimated total diatoms and diatom group totals, survey II, Orange river line, 21–24 September 1950.

relatively large numbers of *Trichodesmium thiebautii*, the filamentous, sometimes colonial blue-green alga most important among the few 'other plants' in these samples, were met with.

Finally, the Orange river line showed an extraordinary reversal of the conditions observed during the first survey, the two diatom-rich stations now being found far beyond the projecting shelf-edge at the outer end of the line. Further, they showed a most extraordinary admixture of species. Though oceanic forms such as *Chaetoceros atlanticum*, *C. peruvianum* and *Planktoniella sol* were among the dominants, the essentially coastal *Chaetoceros compressum* was abundant at station WS 1055. In the

absence of further serial observations to the southward, we can but speculate as to the reasons for this reversal of a feature that remained clear throughout the eleven other series of both surveys. We have seen from the hydrological sections that active upwelling was very pronounced on this line of stations. The stations on the continental shelf lay within the very recently upwelled water, perhaps too recent for extensive plankton production to have got under weigh. The two rich stations were beyond the edge, and may be comparable with those showing secondary offshore increase in phytoplankton on the more northerly series of observations.

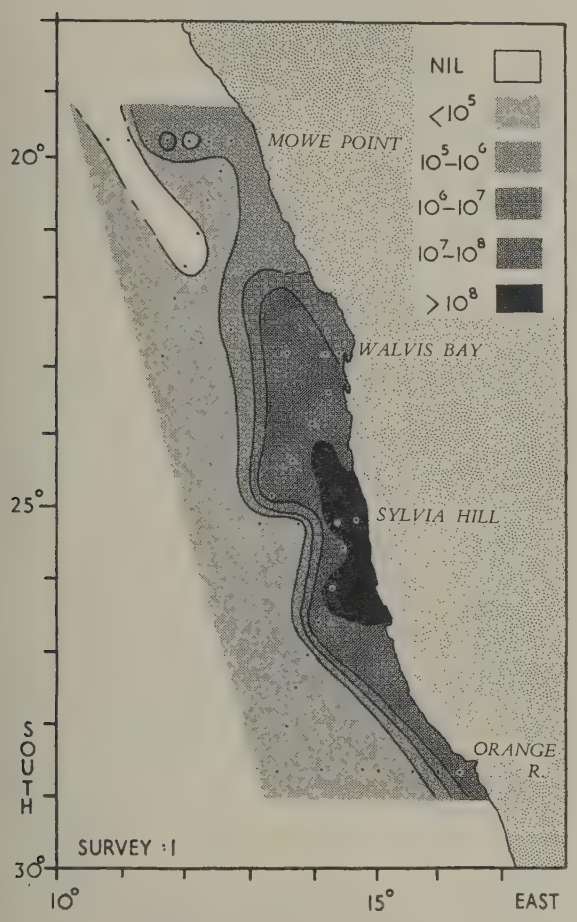

Fig. 81. Distribution of *Chaetoceros*, survey I, March 1950. (Station numbers are shown in Fig. 1.)

Fig. 82. Distribution of *Chaetoceros*, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)

Special distributional features

It is hoped that the following figures are fairly illustrative of the main distributional trends, summarizing the features described in discussing group distributions, and giving examples of the most marked divergences from typical group pattern shown by certain individual species. Most of them are based upon estimated numbers per net haul, contoured logarithmically. Percentage of total diatoms has been used as the criterion for certain categories whose great relative importance in the scanty offshore plankton could not be shown by consideration of their numbers alone. This need arises from their cosmopolitan tendencies permitting them to attain equal or even greater abundance

farther inshore, without, however, forming any significant proportion of the vastly richer vegetation present there (cf. Figs. 93–5).

Figs. 81 and 82 show the outstanding importance of the group Chaetoceraceae in the rich coastal waters during both the seasons studied, and the relative narrowing of that zone in spring as compared with autumn (1st survey). Comparison with Figs. 57 and 65 shows how large a proportion of the total microplankton observed inshore was composed of the members of this one group of diatoms.

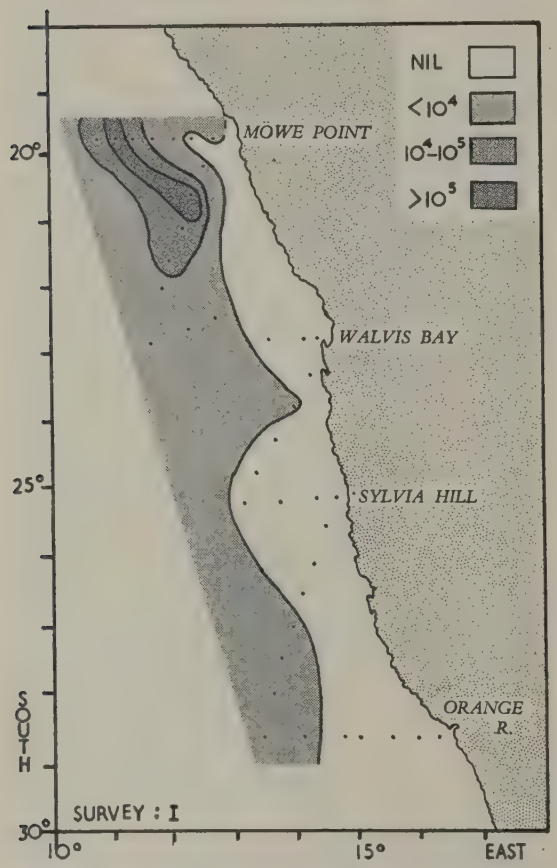

Fig. 83. Distribution of *Planktoniella*, survey I, March 1950. (Station numbers are shown in Fig. 1.)

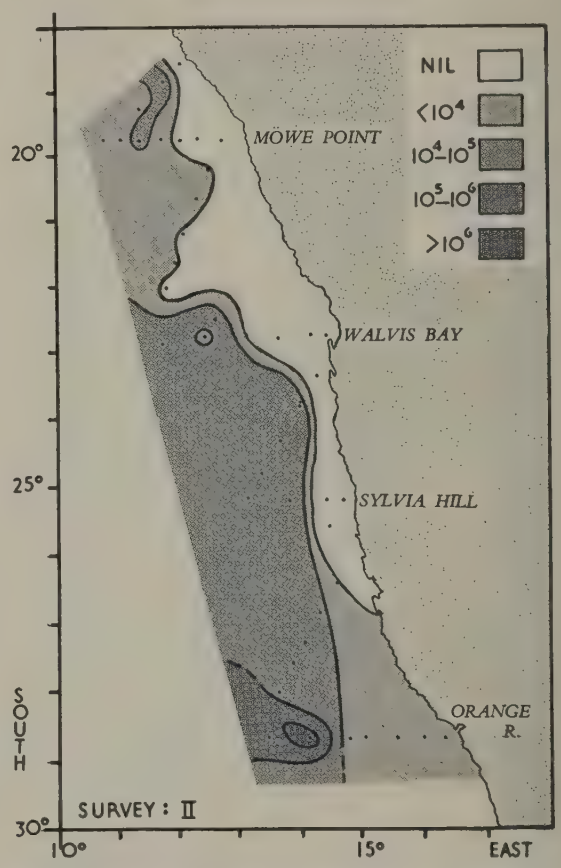

Fig. 84. Distribution of *Planktoniella*, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)

The distribution of the one discoid species found to be most numerous in the scanty offshore phytoplankton—*Planktoniella sol*—is shown in Figs. 83 and 84. The finger-like extensions towards the coast shown near the northern limits of the rich coastal upwelling area seem fairly indicative of actual intrusions of oceanic waters, conforming with hydrological data assessed quite independently (cf. Rayner in Gunther, 1935; Hart, 1953 and Fig. 95 below).

In contrast to *Planktionella* most of the Discineae observed on these two surveys were distributed mainly inshore or over the continental shelf. The distribution of *Stephanopyxis turris*, one of the most numerous of these, is shown in Figs. 85 and 86. It can be seen that though it was clearly an essential coastal form, both in autumn and spring, *Stephanopyxis* was absent from the middle of the *Chaetoceros* zone at both seasons. Further, it was distributed rather more to the northward in spring (Fig. 86)

than in autumn (Fig. 85). This feature cannot be explained by the seasonal shift in temperature alone, for the species is common in coastal waters round Cape Province, to the south of the area surveyed, at most seasons, and indeed all round the coasts of South Africa. A stenohaline tendency, such as that which seems to account for a similar distribution of the dinoflagellate *Dinophysis tripos*, might be partly responsible, since the region from which these species seem to be absent corresponds with the

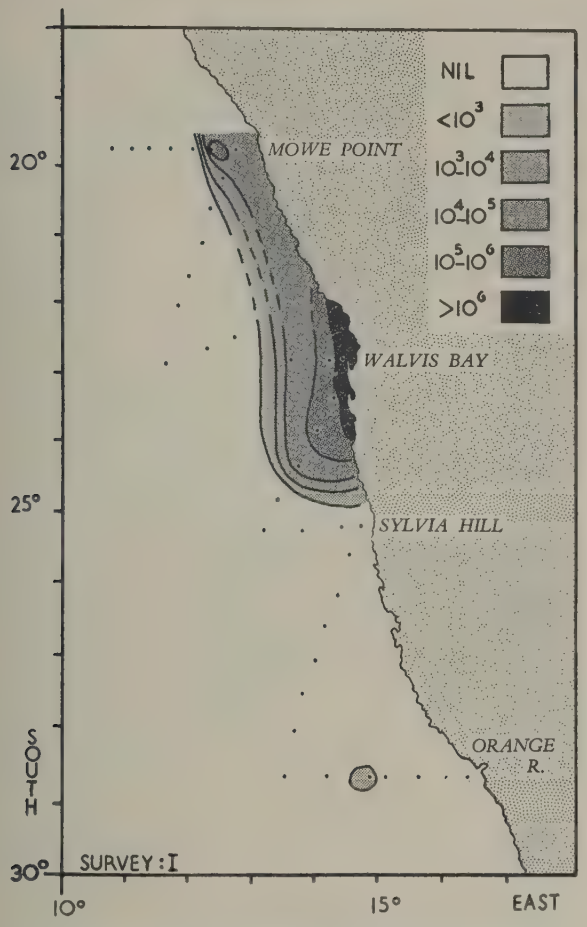

Fig. 85. Distribution of *Stephanopyxis turris*, survey I, March 1950. (Station numbers are shown in Fig. 1.)

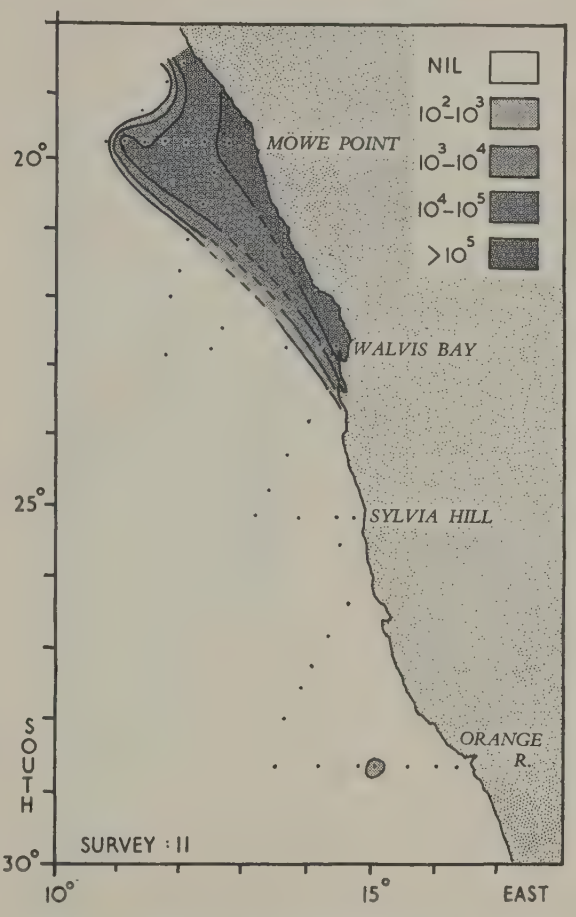

Fig. 86. Distribution of *Stephanopyxis turris*, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)

area of maximum negative salinity anomaly. The reduction in salinity is but slight, however, and *Stephanopyxis* shows so much adaptability elsewhere that an excluding effect of the superabundant chaetocerids, operating physically by crowding and/or chemically by noxious external metabolites (cf. Lucas, 1947) seems a more reasonable hypothesis.

Fig. 87 shows the distribution of *Eucampia zoodiacus* during the first (autumn) survey, when it seemed to be strictly confined to the rich coastal waters from Luderitz Bay northwards. The only Biddulphioid diatom observed in large quantities in any of these samples, the species was not seen at all in spring; when the group—almost exclusively a coastal one—was represented by forms such as *Eucampia cornuta*, *Biddulphia longicruris*, *B. regia* and *Cerataulina pelagica*, irregularly distributed and all in very small numbers. *Eucampia zoodiacus* seems to be a coastal form tending to flourish late in

the succession so far as this region is concerned, its autumn distribution being rather similar to that shown by *Stephanopyxis turris*, but without the apparent inhibition in the richest part of the *Chaetoceros* zone.

Asterionella japonica was the most abundant of the 'Pennatae' in the rich coastal waters, sometimes extending seawards, but in comparatively small numbers, as can be seen from Figs. 88 and 89. It was quite uninhibited by the huge quantities of chaetocerids, among which it flourished during the autumn

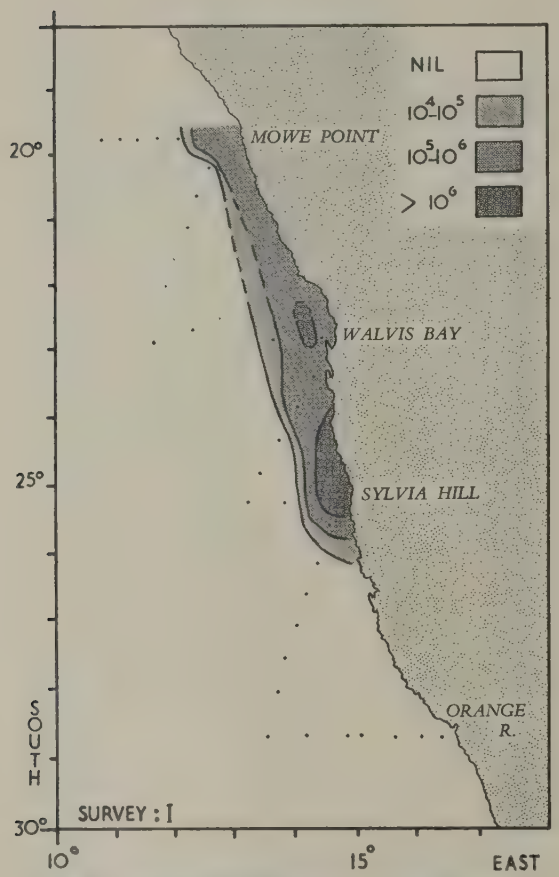

Fig. 87. Distribution of *Eucampia zoodiacus*, survey I, March 1950. (Station numbers are shown in Fig. 1.)

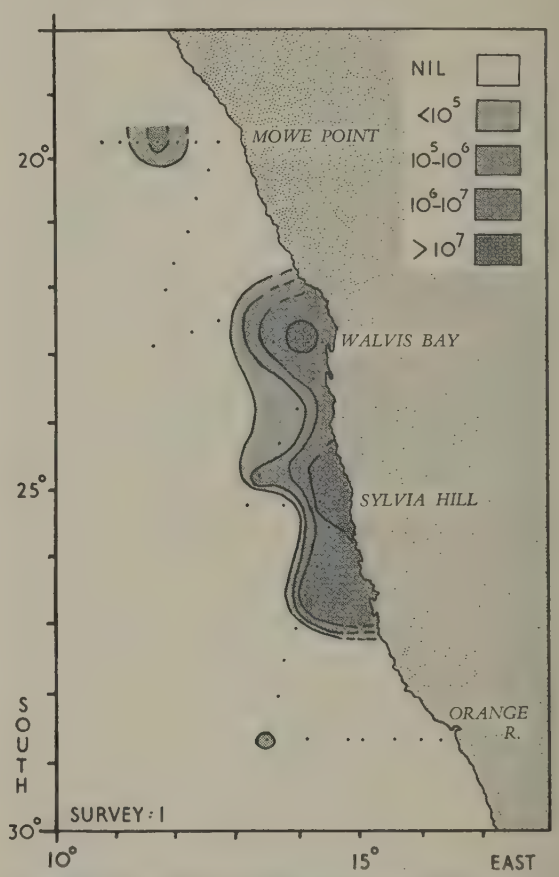

Fig. 88. Distribution of *Asterionella japonica*, survey I, March 1950. (Station numbers are shown in Fig. 1.)

survey. Less numerous, but almost equally widespread in spring. The narrowing of the coastal zone and apparently increased tendency towards fanning-out of the coastal waters in the extreme north of the area at that season were features shown in some degree by other important inshore species.

The distribution of both the species of *Fragilaria* met with is shown in Figs. 90 and 91. *Fragilaria karsteni* proved to be the most strictly coastal of the diatoms encountered in the plankton here during both surveys; one might almost describe it as neritic. Though somewhat less widespread in autumn than it was during the spring survey, the heaviest individual hauls of the species were obtained in autumn near Walvis Bay.

Fragilaria granulata was a species of the outer shelf stations and offshore waters found mainly in

spring. It can be seen that its distribution never overlapped that of *F. karsteni* during these two surveys, and this emphasizes the extent to which the latter can be regarded as an 'indicator' of inshore conditions.

Two abundant 'Pennatae' have not been dealt with in this series: *Nitzschia delicatissima* and *N. seriata*. They tended to be irregularly distributed, perhaps reaching their greatest relative

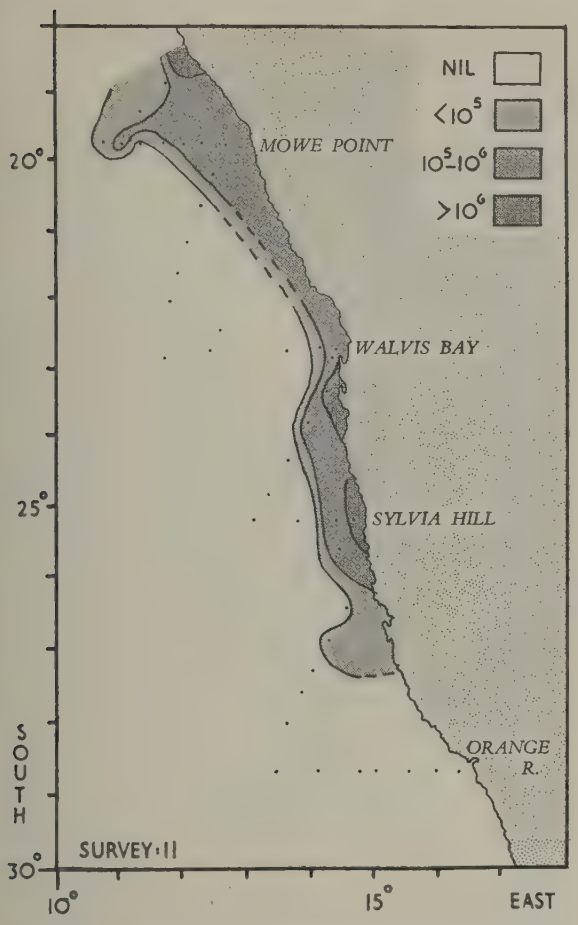

Fig. 89. Distribution of *Asterionella japonica*, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)

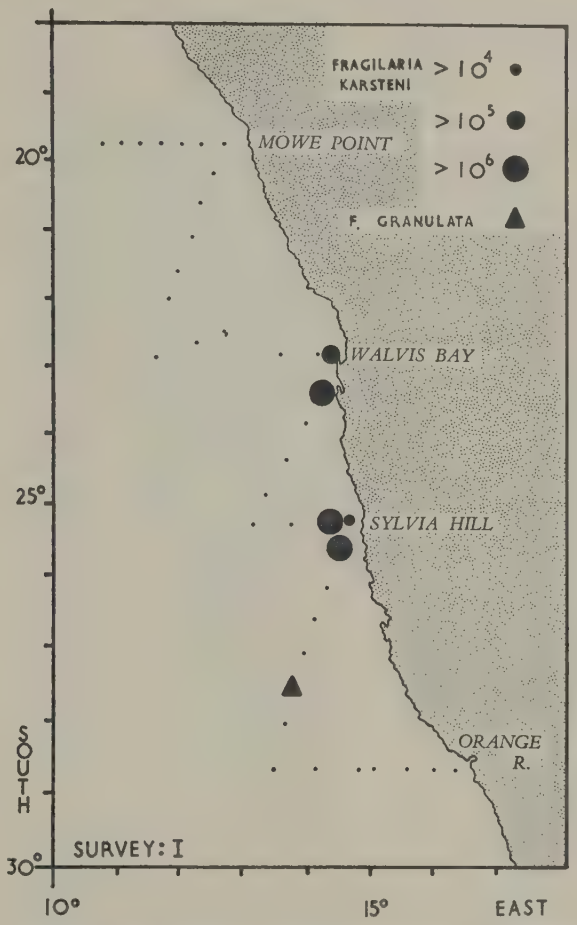

Fig. 90. Distribution of *Fragilaria karsteni* and *F. granulata*, survey I, March 1950. (Station numbers are shown in Fig. 1.)

importance in outer shelf-waters. Since they are among the most completely cosmopolitan of all marine plankton diatoms and, moreover, very difficult to separate with certainty when working at the speed necessary to obtain counts, it is scarcely surprising that they did not show such well-defined distributional trends as most other members of the group.

Figs. 92 and 93 show the relative importance (percentage of total diatoms) of *Thalassiothrix longissima*, the most essentially oceanic of the 'Pennatae' in this area, to be considerable at the offshore stations, where the total phytoplankton was poor. It was equally abundant at some rich shelf stations where, however, its proportion of the whole flora was insignificant.

This same method of treatment was also found necessary to show the high relative importance of the solenoid group offshore during the second survey only. Here they were definitely dominant, and the

offshore flora proved richer at that season than it had been during autumn. Though essentially holoplanktonic, the highly cosmopolitan species concerned easily attain greater numbers nearer land at other times and in other areas, although rarely achieving dominance there. Fig. 94 shows the solenoids as a percentage of total diatoms during the second (spring) survey only. The individual species mainly concerned showed a fairly definite sequence as the survey proceeded from south to north. To the south, far out off Luderitz Bay, *Rhizosolenia alata* was dominant. Proceeding northwards this was

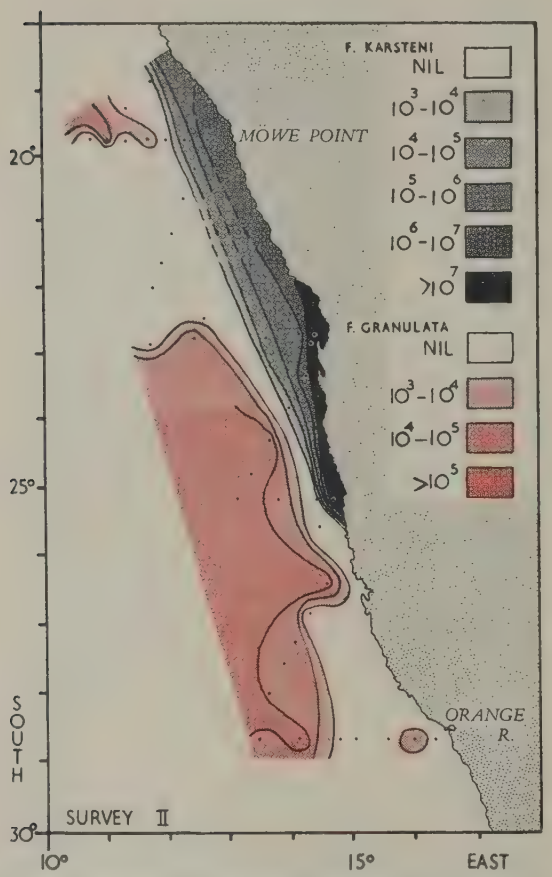

Fig. 91. Distribution of *Fragilaria karsteni* and *F. granulata*, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)

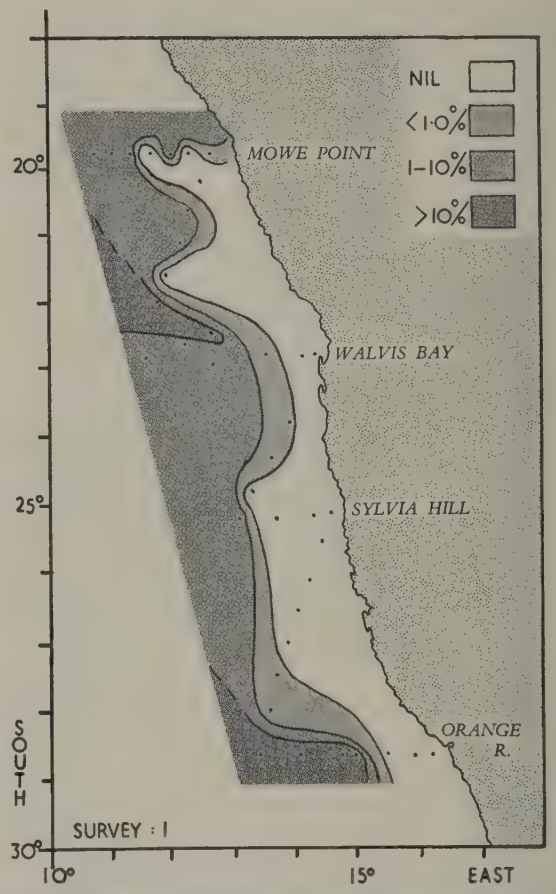

Fig. 92. Distribution of *Thalassiothrix longissima*, survey I, March 1950. Expressed as a percentage of the total diatoms. (Station numbers are shown in Fig. 1.)

succeeded by *R. styliformis*, more or less co-dominant with varying proportions of *R. alata*, these last being superseded in the extreme north of the area studied by *Dactyliosolen mediterraneus*.

In Fig. 95 an attempt has been made to demonstrate another aspect of distributional study, the development of a localized flora where the distinctive offshore and inshore populations most nearly approached each other, near the northern limits of the rich upwelling zone in autumn. The distributions shown are estimated numbers of *Planktoniella sol*, regarded as the characteristic offshore form; *Goniaulax spinifera*, the dinoflagellate predominating in the intervening 'patch';[1] and the estimated

[1] The word 'patch' is here used in its generally accepted sense to describe the area where *Goniaulax* predominated. It is *not* intended to denote exceptional population density as in descriptions of visibly discoloured areas resulting from water-

group totals for the chaetocerids, with their pronounced maximum of development inshore. A degree of overlapping in the horizontal plane seems reasonably accounted for by vertical layering, for which there is some hydrological evidence. The point cannot be established from plankton data alone.

The presence of the *Goniaulax* patch just where the intrusive tongues of oceanic water extend farthest inshore seems strongly suggestive of mixing between the two types of surface-water. Some time-lag—general slowing of dispersive agencies—must also be postulated, to permit development of the third

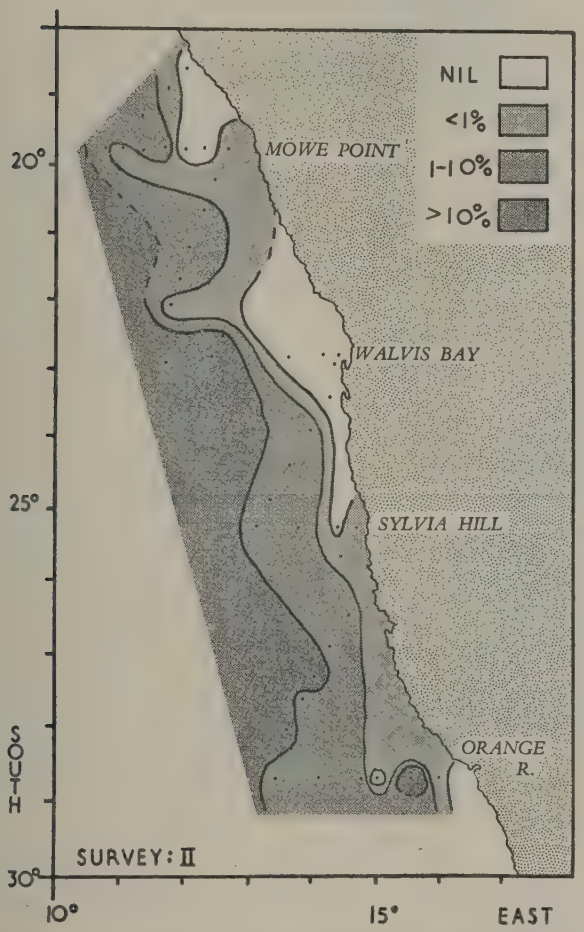

Fig. 93. Distribution of *Thalassiothrix longissima*, survey II, September–October 1950. Expressed as a percentage of total diatoms. (Station numbers are shown in Fig. 2.)

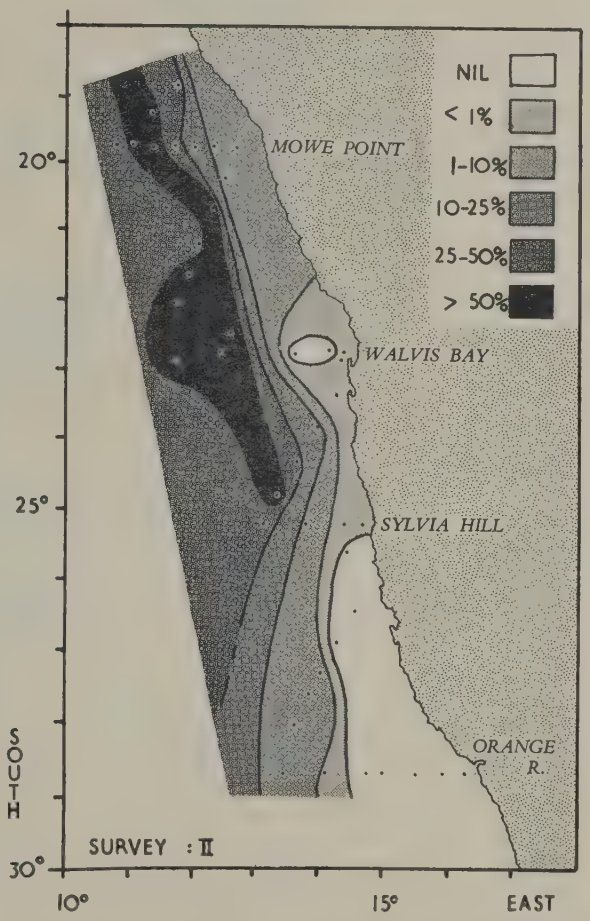

Fig. 94. Distribution of the Soleniineae expressed as a percentage of the total diatoms, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)

distinctive localized type of flora. Much of our evidence points to the prevalence of the conditions required for this immediately prior to the autumn survey. The relatively high stability of the surface-layers, temperature and salinity distribution, and several features of the plant population combine to show that upwelling activity was then much reduced, and the plant succession at or just beyond its peak. Relatively 'old' surface-water from inshore, such as these conditions imply, should mix more readily with the offshore water than would that cooled by recent upwelling.

bloom formation. *Goniaulax* spp. have been known to cause water-bloom elsewhere, but such discoloured water as we were able to sample during these surveys was caused by other organisms. This does not preclude the probability that it may sometimes form blooms in this area—perhaps at other seasons.

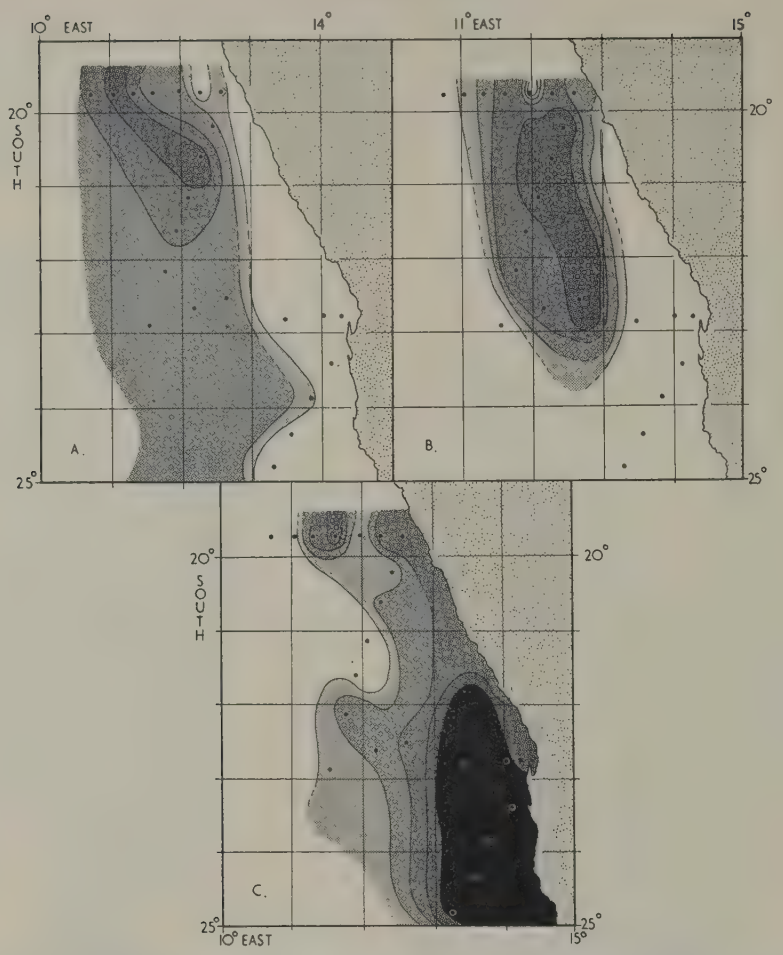

Fig. 95. Distribution of (A) *Planktoniella*, (B) *Goniaulax*, and (C) *Chaetoceros* between Möwe Point and Sylvia Hill, survey I, March 1950. Where there is no shading none was recorded. The lightest shading represents estimates of $< 10^4$ per net haul, the next 10^{4-5}, and so on.

Observations on discoloured water

Large areas of the sea near Walvis Bay were discoloured 'blackish' by diatoms during our first survey, the general appearance being dark green to black, and opaque, very similar to that described in arctic regions by Brown (1868) and found by him to be due to diatoms also. In the Benguela current we found the inshore chaetocerids, especially *Chaetoceros didymum* and *Asterionella japonica*, to be the species chiefly responsible. Within this same region, however, were many more localized brownish or khaki-coloured discolorations, forming irregular bands and streaks roughly parallel with the coast, sometimes associated with foam streaks and lanes of dead and dying macroplankton—mainly ctenophores and salps—at the surface. A minor fish mortality had occurred near Walvis Bay just before we got there.

Three samples from some of these more strikingly discoloured waters were obtained off Sandwich Harbour (about 22° 30′ S. and 10 sea-miles offshore). Subsequent detailed microscopic examination of these yielded the results shown in Tables 18, 19 and 20.

Table 18. *Sample A of discoloured water near Sandwich Harbour. Collected at 13.45 hr. on 9 March 1950. Mixed, fractionized and diluted so that contents of 2·5 ml. could be counted direct, several counts being summed. Factor to reduce numbers to cells/ml.* × *0·4*

Species or category	*No. counted*	× *0·4* ≏ *estimated no. of cells/ml.*	*Estimated area in optical section* μ^2*/ml.*	*Estimated volume* μ^3*/ml.*	*% by number*	*% by area*	*% by volume*
Peridinium triquetrum	387	155	44,795	217,000	40·38	20·53	13·9
Asterionella japonica	324	130	15,600	286,000	33·79	7·15	18·3
Prorocentrum micans	137	55	33,880	374,000	14·33	15·53	23·9
Thalassiosira spp.	52	21	28,000	292,000	5·44	12·83	18·7
Stephanopyxis turris	16	6	17,280	210,000	1·67	7·92	13·4
Peridinium spp.	16	6	74,400	150,000	1·67	34·09	9·6
Chaetoceros didymum	6	2	1,200	9,000	0·63	0·55	0·6
Eucampia zoodiacus	6	2	1,500	8,000	0·63	0·69	0·5
Nitzschia delicatissima	4	2	72	200	0·42	0·03	0·01
Chaetoceros curvisetum	3	1	300	2,200	0·31	0·14	0·1
Small 'Pennatae'	2	—	—	700	0·21	—	0·04
Staphylocystis sp.	2	3	1,200	1,200	0·21	0·55	0·1
Copepod egg	1	—	—	12,000	0·10	—	0·8
Small Dinophyceae non det.	2	—	—	500	0·21	—	0·03
Total Dinophyceae	544	218	153,475	742,700	56·80	70·42	47·53
Total diatoms	411	164	64,252	808,100	43·10	29·44	51·65
Other organisms	1	1	300	12,000	0·10	0·14	0·80
Total microplankton	956	383	218,227	1,562,800	—	—	—

The area in optical section of the total organisms in 1 ml. of this sample, when spread over a Sedgwick-Rafter counting-chamber, would thus be about 500 Whipple's International Standard Units, or 0·2 parts per thousand, and their volume some 1·5 parts per million of water. (The Sedgwick-Rafter cell, 5 × 2 cm. in area and with sides 1 mm. deep, holds 1 ml. of fluid spread over an area of 10 cm. (= $10^9 \mu^2$). One W.I.S.U. is a square 20μ on one side (= 400μ^2). One ml. = ($10^{12} \mu^3$).)

Table 19. *Sample B of discoloured water near Sandwich Harbour. First of two collected at 14.10 hr. on 9 March 1950. Noted as 'Khaki coloured water, reddish at a distance'. 1/8 of 10 ml. of the well-mixed sample, i.e. of 0·55 ml., examined direct by drop method and counts summed. Factor to express results as approx. nos. cells/ml.* × *1·8*

Species or category	*No. counted*	× *1·8* ≏ *estimated no. of cells/ml.*	*Estimated area in optical section* μ^2*/ml.*	*Estimated volume* μ^3*/ml.*	*% by number*	*% by areas*	*% by volume*
Peridinium triquetrum	1,530	2,754	795,906	3,855,600	86·55	80·29	55·34
Asterionella japonica	122	220	26,400	484,000	6·91	2·66	6·95
Eucampia zoodiacus	25	45	33,750	180,000	1·41	3·40	2·58
Small 'Pennatae'	23	41	4,100	32,800	1·29	0·41	0·47
Thalassiosira spp.	22	40	56,000	568,000	1·26	5·65	8·15
Peridinium spp., small	20	36	18,000	813,600	1·13	1·82	11·68
Prorocentrum micans	10	18	11,088	115,200	0·57	1·12	1·65
Stephanophyxis turris	7	13	37,440	455,000	0·41	3·78	6·53
Chaetoceros constrictum	4	7	4,375	22,400	0·22	0·44	0·32
Tintinnidae	2	4	3,600	400,000	0·13	0·36	5·74
Nitzschia delicatissima	1	2	72	200	0·06	0·01	0·01
Cast skins of nauplii	1	2	600	40,000	0·06	0·06	0·57
Total Dinophyceae	1,560	2,808	824,994	4,784,400	88·25	83·23	68·67
Total diatoms	204	368	162,137	1,742,400	11·56	16·35	25·01
Other organisms	3	6	4,200	440,000	0·19	0·42	6·31
Total microplankton	1,767	3,182	991,331	6,966,800	—	—	—

Area in optical section of organisms in 1 ml. in Sedgwick-Rafter counting-chamber: about 2478 W.I.S.U., or nearly 1 part per thousand. Volume nearly 7 parts per million.

Table 20. *Sample C of discoloured water near Sandwich Harbour. Collected immediately after Sample B (Table 19), but in a streak of noticeably more turbid water 'Khaki–coffee coloured'. 0·25 ml. of well-mixed sample examined by drop method and counts summed. Factor to express results as approx. nos. cells/ml. × 4*

Species or category	*No. counted*	*× 4 ≏ estimated no. of cells/ml.*	*Estimated area in optical section μ²/ml.*	*Estimated volume μ³/ml.*	*% by number*	*% by area*	*% by volume*
Peridinium triquetrum	1,363	5,452	1,575,628	7,632,800	88·36	76·13	61·12
Asterionella japonica	74	306	36,720	673,200	4·96	1·77	5·39
Small 'Pennatae'	48	192	19,200	153,600	3·11	0·93	1·23
Peridinium spp.	10	40	258,000	904,000	0·65	12·47	7·24
Thalassiosira spp.	9	36	50,400	511,200	0·58	2·43	4·09
Chaetoceros constrictum	7	28	17,500	89,600	0·45	0·85	0·72
Stephanopyxis turris	6	24	69,120	840,000	0·39	3·34	6·73
Nitzschia delicatissima	6	24	864	2,400	0·39	0·04	0·02
Chaetoceros compressum	5	20	8,800	40,000	0·32	0·42	0·32
Prorocentrum micans	4	16	9,856	102,400	0·26	0·48	0·82
Chaetoceros dichaeta	3	12	4,800	108,000	0·19	0·23	0·86
Eucampia zoodiacus	2	8	6,000	32,000	0·13	0·29	0·26
Tintinnidae	2	8	7,200	800,000	0·13	0·35	6·40
Rhizosolenia setigera	1	4	5,600	600,000	0·06	0·27	4·80
Total Dinophyceae	1,377	5,508	1,843,484	8,639,200	89·27	89·08	69·18
Total diatoms	161	654	219,004	3,050,000	10·58	10·57	24·42
Other organisms	2	8	7,200	800,000	0·13	0·35	6·41
Total microplankton	1,540	6,170	2,069,688	12,489,200	—	—	—

Area in optical section of the organisms in 1 ml. in Sedgwick-Rafter counting-chamber: about 5160 W.I.S.U., or 2+ parts per thousand. Volume about 12·5 parts per million.

These tables allow comparisons, not only of the constituents, but also of the relative density of the microplankton in each sample in terms of numbers, area in optical section, and volumes, per millilitre. It is seen that sample *C* (Table 20) was by any standard nearly twice as dense as *B*. Sample *A* was much thinner, but the ratio varied little in terms of numbers, area or volume.

As to the constitution of the samples it appears that the small dinoflagellates *Peridinium triquetrum* and *Prorocentrum micans* were the main constituents of the thinnest of these samples (Table 18). with quite a high proportion of *Asterionella* and other inshore diatoms. The two richer samples (Tables 19 and 20) show a definite 'bloom' of *Peridinium triquetrum*, the other constituents providing less than 12% of the total number of organisms estimated.

Peridinium triquetrum, a neritic species of very wide distribution, has been recorded 'blooming' in association with a fish mortality on at least one previous occasion, at Rostock in the Baltic on 10 October 1917 (Lindemann, 1924, who called it by its old name *Heterocapsa triquetra*). Lindemann's plankton observations were only made after a considerable search for other possible causes of the catastrophe had proved fruitless. The *Peridinium triquetrum* was co-dominant with *Krypto-peridinium foliaceum* and other microplanktonic organisms were present only in quite insignificant proportions.

Our Benguela current findings, added to Lindemann's observations, might seem to suggest *Peridinium triquetrum* as a probable 'cause' of the Walvis Bay mortalities, but it has to be remembered that in both instances the mortality had begun before the observations on the bloom were made. The bloom may or may not have been present when the fish were killed. Braarud (1945) has shown that very high production of *P. triquetrum* (and sometimes of *Prorocentrum* also) may occur in heavily

polluted waters, inimical to most other marine plankton organisms, in the inner Oslo Fjord. Thus it even seems possible that these blooms might be the result, rather than the cause, of the mortalities.

The seemingly conflicting statements on the nature of the discolorations so often seen near Walvis Bay do seem to be partially resolved by our observations. Gilchrist's (1914) early insistence upon the vast proliferations of diatoms in the area are amply confirmed. Then to the dinoflagellate blooms described above we can add one of ciliate Protozoa (considerably to the northward but still within the Benguela current area) which was sampled at the end of the second survey. Further we have little doubt that Marchand's contention that blooms due to *Noctiluca miliaris* also occur there will eventually be vindicated.[1]

In the past each commentator has tended to assume that the most recently identified bloom-forming organism was responsible for all the other macroscopically similar visual effects reported from the area. This was natural enough when direct observations were few and often obscurely recorded. The point which we can claim from our results is that blooms—visible discolorations—due to widely differing types of organisms may occur (mostly at different times no doubt) within the same relatively small sea area.

The estimates of area and volume of the bloom-forming organisms in Tables 18–20 have been made from the means of numerous measurements and approximation to the nearest geometrical figure. They do not pretend to be precise, but are unlikely to show positive error. They are given here in the hope that the relative quantities of plant substance represented by counts of the various species may be better appreciated with their aid. The areas in particular may interest those familiar with Whipple's ([1889], 1908) concept of the International Standard Unit, a square 20 μ on the side viewing the organisms in optical section, which was found very useful in practical limnological work. These findings suggest that it could be very useful in marine work also, but it has to be borne in mind that it is only in the study of these blooms (or in cultures) that the marine plankton worker ever encounters populations approaching the densities shown in Tables 18–20. Usually he has to deal with populations sparser by at least one order of magnitude than these. It is in fresh waters that such concentrations are frequently met with.

From the volumes the relative size relations of the more important plants found in these samples can be computed, with the results shown in Table 21. This shows, for example, that here one cell of the diatom *Stephanopyxis turris* was roughly eleven times as big as one cell of *Chaetoceros constrictum*, and twenty-five times as big as one of the dominant dinoflagellates, *Peridinium triquetrum*. Obviously it is important to establish dominance by methods going further than the counts alone when possible. Lohmann (1908) made an attempt in this direction by analogous methods in Kiel Bay, but generally speaking the range of size variation, even within single species of phytoplankton organisms, is so great that application of the method to large series would demand recalculation of volume factors every few samples, and the increase in time and labour involved would make it quite impracticable.

An intense red discoloration observed close inshore (WS 1107) in 13° 05′ S. at the conclusion of the second survey proved to be due to swarming of a ciliate protozoan *Cyclotrichium meunieri* Powers (probably synonymous with *Halteria rubra* Lohmann = *Mesodinium rubrum* Lohmann (Apstein).) Large-scale discolorations caused by this organism had previously been seen in the waters round Cape Peninsula (Hart, 1934).[2] When swarming this animal distorts itself or bursts spontaneously in

[1] *Trichodesmium thiebautii*, the Cyanophycean that so often forms blooms in many parts of the tropical and subtropical Atlantic, probably does so in the Benguela current area on occasions. It was dominant in some of our poorer plankton hauls, but we have not yet seen it there in bloom-forming quantities.

[2] An unfortunately premature communication, missing Lohmann (1908), Apstein (1908), Paulsen (1909) and even Darwin (1839). I tried to rectify these mistakes in a second letter published in 1943, but cannot blame myself for having missed Powers (1932). Our ship left Europe in 1933 when his work had barely had time to reach European libraries, and being

any quantity of water small enough to permit one to examine it microscopically, the process being accentuated in greater or less degree by addition of all the narcotics or fixatives tried hitherto. Bary and Stuckey (1953) found very dilute hydrogen peroxide the best narcotic, leaving a larger minority of relatively little distorted specimens available for subsequent fixation. When the ciliates burst many of the coloured 'platelets' (Lohmann)[1] are extruded. The enormous numbers of these in the sample from WS 1107 were observed in the field by Clarke and Currie, and their likeness to Hematococcidae noted. The preserved sample, however, showed the characteristically shrunken remains of many of the ciliates that had not burst (cf. Lohmann, 1908, fig. 7, no. 53, p. 201), so many indeed, that the discoloured water must have contained not less than 13,370 per ml. It seemed pointless to attempt counting of the freed 'platelets' since the vast majority had unquestionably been aggregated (in varying numbers) within ciliates before the sample was taken. A small *Gymnodinium* sp., one other small dinoflagellate and a *Coscinodiscus* sp. were present in very small numbers (up to 7 per ml.).

Table 21. *Size inter-relations of organisms from the samples taken off Sandwich Harbour, 9 March 1950. Selected to cover the dominants and species covering the extremes of variation in volume; others omitted*

	Rhizosolenia setigera	*Stephanopyxis turris*	*Thalassiosira* spp.	*Chaetoceros dichaeta*	*Prorocentrum micans*	*Chaetoceros constrictum*	*Peridinium triquetrum*	*Approx. volume (estimated) in* μ^3 ($1\ \mu^3 = 10^{-12}$ *ml.*)
Rhizosolenia setigera	1	4	10½	16½	23	47	107	150,000
Stephanopyxis turris	4	1	2½	4	6	11	25	35,000
Thalassiosira spp.	10½	2½	1	1½	2	4½	10	14,200
Chaetoceros dichaeta	16½	4	1½	1	1½	3	6	9,000
Prorocentrum micans	23	6	2	1½	1	2	4½	6,400
Chaetoceros constrictum	47	11	4½	3	2	1	2	3,200
Peridinium triquetrum	107	25	10	6	4½	2	1	1,400

Dense swarms of this ciliate have thus been seen near the two ends of the region where the Benguela current is best defined. It seems unlikely from what is known of its proclivities elsewhere, that the conditions of negative anomaly of temperature and salinity in between would prove exclusive to it. Probably, therefore, before long some more fortunate observer will be able to add it to the list of diverse forms now known to give rise to visual discolorations there at various times.

The distinction between offshore and inshore diatom floras

Yet another array of the data, based upon arbitrarily selected distance limits, serves to show up the distinctive features of the flora of the inshore and offshore waters during the two surveys, providing a basis for ecological characterization of the species within each of the main diatom groups. Some repetition of points made in discussing distribution at group level is involved here, but seems to the writer (T.J.H.) to be unavoidable if the apparent anomalies due to the cosmopolitan and panthalassic species are to be made clear.

The arbitrary limits first chosen were: stations within 40 miles from the coast regarded as within an inshore region, and stations more than 100 miles from the coast, regarded as definitely oceanic or

without fore-knowledge that we were to encounter his ciliate more than a year later, we could hardly be expected to have included it in the small working library carried at sea! I have hoped to clear up some of the misunderstandings following my 1934 letter in a separate publication, but the topic seems dangerous! (T.J.H.).

[1] These were described as 'most probably symbiotic algae', and given the name *Erythromonas haltericola* by Lohmann (1908). Concerning them also Apstein (1908) wrote 'this is perhaps the alga living symbiotically in *Mesodinium rubrum*'. I mentioned them as 'Coloured granules some 4μ in diameter, possibly symbiotic zoochlorellae' in ignorance of the earlier work, though this may now seem to be incredible (T.J.H.).

offshore. It then became clear that the results from the wide intermediate or 'outer shelf' zone (40–100 miles from the land), besides yielding the obvious intermediate averages, also showed up the extent to which surface-waters of the two more distinctive types were overstepping the arbitrary limits chosen on each of the two surveys. The full value of this feature could only be realized by considering individual species on each line of stations as we have already treated the main groups. Though this is impracticable here it still seemed worthwhile to include average values for the arbitrary 'outer shelf' zone, despite the masking effect of the 'averaging' process in the following tables, for the reason given above.

For this special purpose the anomalous results from the Orange river line were not considered, and this leaves thirty-two stations at repeat positions on each of the two surveys for comparison.

Table 22 shows the average estimated diatom totals per net haul, and the average totals and percentages for each main group as previously defined, when the data are arrayed in this fashion. It also provides in effect a crude summary of the line-upon-line treatment of main group-distribution already given. It is essential that the relative quantities indicated should be kept in mind if the percentages for species within each group, given in Tables 13–17, are to be properly understood.

Table 22. *Average estimated diatom totals, with average numbers and percentages of the main diatom groups, when the data are grouped according to distance from the coast as shown. (Results from the Orange river line excluded)*

	Average estimate of total diatoms per net haul	*Average Discineae*		*Average Biddulphiineae*		*Average Chaetoceraceae*		*Average Soleniineae*		*Average 'Pennatae'*	
		Numbers	%	*Numbers*	%	*Numbers*	%	*Numbers*	%	*Numbers*	%
Inshore stations <40 sea miles from the coast											
First survey (autumn)	85,157,491	2,836,753	3·33	1,528,631	1·80	68,024,177	79·88	877,582	1·03	11,890,348	13·96
Second survey (spring)	65,979,818	884,173	1·34	72,400	0·11	58,486,700	88·64	146,455	0·22	6,390,090	9·68
'Outer shelf' stations 40–100 sea miles from the coast											
First survey (autumn)	15,712,563	217,934	1·39	14,672	0·09	14,673,800	93·39	80,419	0·51	725,738	4·62
Second survey (spring)	2,158,972	82,025	3·80	225	0·01	811,229	37·57	727,091	33·68	538,402	24·94
Offshore stations >100 sea miles from the coast											
First survey (autumn)	156,287	20,972	13·42	None seen	—	22,480	14·38	31,510	20·16	81,323	52·03
Second survey (spring)	779,740	17,880	2·29	None seen	—	139,260	17·86	515,400	66·10	107,200	13·75

From Table 22 it appears that:

(1) the **Discineae** were of minor importance offshore during the first (autumn) survey. Elsewhere they formed but a small proportion of the total diatoms, their greater numbers inshore notwithstanding during both surveys.

(2) The **Biddulphiaceae** were of very minor importance inshore, mainly in autumn. Very small quantities of this group were observed on the 'outer shelf', and none at the offshore stations.

(3) The **Chaetoceraceae** were strongly dominant inshore at both seasons, rather more so in spring than in autumn. They were also strongly dominant on the 'outer shelf' in autumn, but much less so during spring. Offshore they were outnumbered by other groups at both seasons.

(4) The **Soleniineae** were the dominant group offshore during spring. They ranked second to

the chaetocerids on the 'outer shelf' in spring, and to the 'Pennatae' offshore in autumn. Inshore they were relatively unimportant at both seasons.

(5) The 'Pennatae', though generally much less abundant than the chaetocerids, ranked second to that group at the inshore stations during both surveys. They were rather more important in autumn than in spring right inshore, but this trend was reversed on the 'outer shelf'. Offshore the group was relatively much more important in autumn than during spring, although slightly more abundant in the richer spring catches.

Table 23. *Relative importance of the group Discineae, and percentage of the several species, within the group. Results arrayed according to distance from the land as shown, omitting those from the Orange river line*

	Inshore *< 40 sea-miles from land*		*'Outer shelf'* *40–100 sea-miles from land*		*Offshore* *> 100 sea-miles from land*	
	First survey (autumn)	*Second survey (spring)*	*First survey*	*Second survey*	*First survey*	*Second survey*
(*a*) Average total diatoms	85,157,491	65,979,818	15,712,563	2,158,972	156,287	779,740
(*b*) Average total Discineae	2,836,753	884,173	217,934	82,025	20,972	17,880
b/*a* as percentage	3·33	1·34	1·38	3·80	13·44	2·29
Average total for each category as percentage of the average total for the group (*M* category/*b* as %)						
Skeletonema costatum	—	1·56	1·15	—	—	—
Stephanopyxis turris	16·0	6·46	2·52	12·12	—	—
Thalassiosira condensata	2·8	—	0·92	—	—	—
T. excentrica	19·5	—	11·41	—	45·0	—
T. hyalinum	6·9	—	0·16	—	—	—
T. rotula	13·8	—	—	—	—	—
T. subtilis	27·2	50·43	70·63	11·82	—	6·0
Thalassiosira spp. non det.	13·3	34·73	2·75	23·20	—	30·2
Bacterosira fragilis	0·03	—	—	—	—	—
Coscinodiscus gigas	—	—	—	—	0·3	—
C. janischii	< 0·01	—	—	—	—	—
Coscinodiscus spp. non det	0·34	5·61	0·20	14·85	—	9·8
Actinocyclus spp. non det.	0·01	—	—	—	—	—
Planktoniella sol	0·02	0·11	9·84	32·15	54·7	47·3
Hemidiscus cuneiformis	—	0·03	0·01	0·46	—	—
Actinoptychus senarius	< 0·01	0·15	0·01	0·64	—	6·7
Asterolampra spp. non det.	—	0·41	—	—	—	—
Asteromphalus heptactis	0·08	0·49	0·40	4·76	—	—

Table 23, which shows the relative importance of the various Discineae when the data are grouped in this fashion, provides strong evidence of the neritic or inshore habit of most of the species. Though several extended to the outer shelf, eleven out of the eighteen categories were not seen farther offshore. *Planktoniella sol* was clearly the most essentially oceanic species. Although sufficiently adaptable to occur inshore its numbers increased very markedly with increasing distance from land during both surveys. The remainder of the scanty offshore representation of the group consisted chiefly of more panthalassic, but equally cosmopolitan, species like *Thalassiosira excentrica* and *T. subtilis*.

The most important Discineae inshore were *Stephanopyxis turris* and various species of *Thalassiosira*. They were most prominent in autumn (or late in the succession) while the less numerous forms provided greater *relative* proportions of the group totals in the smaller spring catches (e.g. *Asteromphalus heptactis*).

The Biddulphiaceae (Table 24) were very sparsely represented in the area surveyed. Inshore, in autumn, *Eucampia zoodiacus* was of some slight importance, and just extended on to the outer shelf area. There, however, *Cerataulina pelagica* formed a slightly higher proportion of the very small group average. *Eucampia zoodiacus* was not observed during the spring survey, when *Biddulphia longicruris* provided the bulk group totals. Biddulphiaceae were not observed more than 100 miles offshore during either survey, though one of the species recorded, *Hemiaulus hauckii*, has been seen far out in the South Atlantic on other occasions, and should probably be regarded as an oceanic form.

Table 24. *Relative importance of the group Biddulphiaceae, and percentage of the several species within the group. Results arrayed according to distance from the land as shown, omitting those from the Orange river line*

	Inshore <40 sea-miles from land		*'Outer shelf' 40–100 sea-miles from land*		*Offshore >100 sea-miles from land*	
	First survey (autumn)	*Second survey (spring)*	*First survey*	*Second survey*	*First survey*	*Second survey*
(*a*) Average total diatoms	85,157,491	65,979,818	15,712,563	2,158,972	156,287	779,740
(*b*) Average total Biddulphiaceae	1,528,631	72,400	14,672	225	—	—
b/*a* as percentage	1·80	0·11	0·09	0·01	—	—
Average for each category as % of (*b*)						
Biddulphia longicruris	—	99·05	—	—	—	—
Cerataulina pelagica	1·66	0·95	53·04	—	—	—
Triceratium favus	0·02	—	—	—	—	—
Hemiaulus hauckii	—	—	1·38	—	—	—
Eucampia cornuta	—	—	—	100	—	—
E. zoodiacus	98·32	—	45·58	—	—	—

The tremendous local importance of the Chaetoceraceae is clear from Table 25, which also illustrates the very cosmopolitan nature of the species of this family. All of those which we were able to identify are widely known from other regions, ranging from 'boreal' to 'warm temperate', with some which extend into truly tropical surface-waters as well.

Within this area most of them were essentially neritic—inshore and outer shelf species—and of these a majority were more abundant in autumn, or late in the succession, than in spring. Most important of all, however, were three panthalassic species which must be among the most widespread and abundant of all marine plankton diatoms: *Chaetoceros compressum*, *C. constrictum* and *C. curvisetum*. The first two of these were almost equally abundant at both seasons, while *C. curvisetum*, the most numerous of all the diatoms according to these estimates, showed a distinct maximum in spring, though vast numbers had been found in the autumn samples also.

Of the more strictly neritic species *C. didymum* was the most abundant, especially in autumn, when vast numbers of the very characteristic resting spores were present. *C. subsecundum* and most of the other neritic species of lesser but still considerable local importance, for example, *C. affine*, *C. costatum*, *C. debile*, *C. teres*, *C. tetras*, showed a similar time distribution. *C. strictum*, however, showed a strong inshore maximum during the spring survey.

The most abundant and widespread of the oceanic species, *C. convolutum*, showed a spring maximum here. So also did two oceanic forms of lesser importance in these samples: *C. atlanticum* and *C. peruvianum*.

The 'ecological characterization' of the species of this most important and difficult genus of marine plankton diatoms arrived at by the late Professor Gran, through continued efforts towards improving his system of 'plankton elements' as applied in the northern hemisphere (Gran in Murray and Hjort, 1912; Gran and Braarud, 1935), can thus far be extended to this southern area without serious

discrepancy. Two well-known cosmopolitan species, however, were found to be distributed here rather differently from what might have been expected from their previously known dispositions elsewhere. *C. lorenzianum*, usually regarded as a neritic form, here reached its greatest relative importance in the offshore samples, with a strong spring maximum. Conversely *C. decipiens*, one of the most widespread of all oceanic species, was more plentiful here inshore in spring than it had been offshore during the autumn survey.

Table 25. *Relative importance of the group Chaetoceraceae, and percentage of the several species within the group. Results arrayed according to distance from the land as shown, omitting those from the Orange river line*

	Inshore <40 sea-miles from land		*'Outer shelf' 40–100 sea-miles from land*		*Offshore >100 sea-miles from land*	
	First survey (autumn)	*Second survey (spring)*	*First survey*	*Second survey*	*First survey*	*Second survey*
(*a*) Average total diatoms	85,157,491	65,979,818	15,712,563	2,158,972	156,287	779,740
(*b*) Average total Chaetoceracea	68,024,177	58,486,700	14,673,800	811,229	22,480	139,260
b/*a* as percentage	79·87	88·64	93·41	37·58	14·40	17·86
Average for each category as percentage of the average total for the group (*M* category/*b* as %)						
Chaetoceros affine	0·12	1·67	1·32	1·00	—	—
C. atlanticum	—	<0·01	—	3·09	—	3·66
C. compressum	14·18	18·70	42·92	37·91	26·69	17·23
C. constrictum	21·76	11·65	13·59	22·06	—	23·48
C. convolutum	0·01	<0·01	0·33	3·93	10·68	11·25
C. costatum	0·79	—	1·10	0·19	—	—
C. curvatum	—	—	0·01	—	—	—
C. curvisetum	22·12	45·67	3·57	6·92	56·94	21·97
C. debile	4·60	0·41	0·45	—	—	—
C. decipiens	0·36	5·05	0·08	5·21	4·89	—
C. didymum	5·93	1·89	1·96	0·98	—	1·29
C. didymum (resting spores)	13·57	0·02	6·99	—	—	—
C. difficile	1·63	1·35	5·48	1·48	—	1·48
C. holsaticum	—	0·34	—	—	—	—
C. imbricatum	—	—	0·25	—	—	—
C. laciniosum	<0·01	0·02	—	—	—	—
C. lorenzianum	0·31	0·85	—	5·17	—	17·92
C. peruvianum	0·05	—	0·05	0·29	—	0·60
C. pseudocrinitum	0·13	—	6·05	—	—	—
C. sociale	—	0·39	0·37	—	—	2·58
C. strictum	1·84	10·93	3·98	2·09	—	—
C. subsecundum	6·28	0·30	1·20	9·68	—	—
C. subsecundum (resting spores)	0·22	—	—	—	—	—
C. teres	1·04	<0·01	3·98	—	—	—
C. tetras	0·11	0·66	2·37	—	—	—
C. van heurckii	4·95	0·10	1·39	—	0·80	—
Chaetoceros spp. non det.	—	—	2·57	—	—	—

This evidence of a more panthalassic trend than was hitherto suspected for these two species, in a region of exceptionally steep temperature gradients and rapid changes in conditions of the milieu, is not surprising. Indeed, the general conformity of the majority of the genus to the distributional pattern that might have been predicted from their known proclivities elsewhere, seems even more remarkable to me under these conditions, which seem quite sufficient to account for the occurence of both warm-water and cold-water forms together within a limited area. When the need for a reasonable

amount of elasticity in the application of the ecological terms is borne in mind, the value of the earlier work seems to me most amply justified (T.J.H.).

Within the group Soleniineae, consisting almost wholly of holoplanktonic cosmopolitan forms, the difficulty involved in any attempt at further ecological characterization is augmented by the almost completely panthalassic nature of some of the most important species. This results in some species showing maximum importance offshore under oceanic conditions in spring, but inshore under neritic conditions in autumn or vice versa. The compromise implicit in the word panthalassic seems as far as one can go in any attempt at brief summary of their distributional tendencies!

Table 26. *Relative importance of the group Soleniineae, and percentage of the several species within the group. Results arrayed according to distance from the land as shown, omitting those from the Orange river line*

	Inshore *< 40 sea-miles from land*		*'Outer shelf'* *40–100 sea-miles from land*		*Offshore* *> 100 sea-miles from land*	
	First survey (autumn)	*Second survey (spring)*	*First survey*	*Second survey*	*First survey*	*Second survey*
(*a*) Average total diatoms	85,157,491	65,979,818	15,712,563	2,158,972	156,287	779,740
(*b*) Average total Soleniineae	877,582	146,455	80,419	727,091	31,510	515,400
b/*a* as percentage	1·03	0·22	0·51	33·68	20·16	66·10
Average for each category as percentage of the average total for the group (*M* category/*b* as %)						
Bacteriastrum hyalinum	0·21	—	1·17	—	—	—
B. varians	0·16	—	—	0·02	—	—
Rhizosolenia alata	1·83	0·41	36·78	21·11	36·92	8·67
R. cylindrus	—	—	—	0·02	—	—
R. fragillissima	—	—	0·58	—	—	—
R. hebetata	9·34	0·76	49·94	5·40	49·62	4·85
R. imbricata	1·08	0·19	1·63	2·11	3·81	2·25
R. robusta	0·05	—	0·06	—	—	—
R. setigera	—	66·29	—	3·09	—	0·12
R. simplex	—	—	5·80	0·67	9·65	—
R. stolterfothii	0·74	—	—	—	—	—
R. styliformis	0·13	0·60	0·45	30·25	—	74·69
Guinardia sp. non det.	—	—	0·09	—	—	—
Leptocylindrus danicus	15·88	4·66	2·72	—	—	—
Dactyliosolen mediterraneus	70·53	2·23	—	36·90	—	9·19
Corethron criophilum	0·05	24·86	0·77	0·43	—	0·23

A few species, notably *Leptocylindrus danicus* with its maximum late in the succession, were definitely limited to the neritic samples in both series. *Rhizosolenia setigera*, seen only during the spring survey, was important inshore at that season.

The most completely cosmopolitan species, that helped to render this group dominant offshore in spring and of considerable importance there in autumn also, should probably be regarded as essentially oceanic, but so adaptable that they may attain higher numbers among the vastly heavier catches of other forms in enriched coastal waters on some occasions. A similar difficulty is found when one attempts ecological classification of some of the dominant phytoplankton species of antarctic surface waters (Hart, 1942).

In the Benguela current area the important panthalassic solenoids were: *Rhizosolenia alata* and *R. hebetata*, especially late in the succession inshore, but also augmenting the group's spring maximum offshore; *R. styliformis*, here showing a more distinct oceanic trend and spring maximum; and

Dactyliosolen mediterraneus. This last provides the greatest enigma, being found in great numbers inshore during the first (autumn) survey, but also among the dominants on the outer shelf and offshore (especially in the northern part of our area) in spring. It is possible that more restricted temperature requirements may account for this anomaly if the spring temperatures inshore are suboptimal for this species. Conversely, *Corethron criophilum*, undoubtedly an oceanic form in most of its phases, here showed a very definite maximum inshore in spring, which might be explained by 'preference' for lower temperatures.

The ecological relationships of the 'Pennatae' (Table 27) at group level are not very clear, chiefly because it is an arbitrary 'unnatural' assemblage of the diverse 'reversionary plankton forms' with sundry tychopelagic species, introduced solely to assist in concentrating the data to within manageable proportions. At the specific level, however, most of them can be seen to conform to definite distributional trends much more clearly than most of the solenoids.

Fragilaria karsteni, *Asterionella japonica* and the rarer tychopelagic species all had a definitely inshore, neritic distribution. *Fragilaria karsteni* was most abundant in spring and *Asterionella japonica* in autumn. *Thalassiothrix longissima* was an offshore form with a spring maximum, and so in the main was *Fragilaria granulata*, which never overlapped its congener.

The only important 'Pennatae' not clearly assignable to one of the distributional trends that we now feel to be recognizable (somewhat dimly, perhaps) are *Nitzschia delicatissima* and *N. seriata*. These are among the most ubiquitous, cosmopolitan, panthalassic diatoms known, as all marine plankton workers must agree. Here they were prominent at all distances from land especially in spring. *N. seriata* was the more important inshore, while *N. delicatissima* showed maximum relative importance in the scanty offshore catches in autumn, though not nearly so numerous there as it was on the 'outer shelf' during both surveys.

Table 27. *Relative importance of the group Pennatae, and percentage of the several species within the group. Results arrayed according to distance from the land as shown, omitting those from the Orange river line*

	Inshore *<40 sea-miles from land*		*'Outer shelf'* *40–100 sea-miles from land*		*Offshore* *>100 sea-miles from land*	
	First survey (autumn)	*Second survey (spring)*	*First survey*	*Second survey*	*First survey*	*Second survey*
(*a*) Average total diatoms	85,157,491	65,979,818	15,712,563	2,158,972	156,287	779,740
(*b*) Average total 'Pennatae'	11,890,348	6,390,090	725,738	538,402	81,323	107,200
b/*a* as percentage	13·96	9·68	4·62	24·94	52·03	13·75
Average for each category as percentage of the average total for the group (*M* category/*b* as %)						
Fragilaria granulata	—	0·18	0·06	9·95	—	6·04
F. karsteni	12·77	48·95	—	0·21	—	—
Asterionella japonica	64·15	5·42	62·78	6·01	—	3·36
Thalassiothrix longissima	0·06	1·54	6·12	18·60	31·24	29·04
Thalassionema nitzschioides	—	4·35	0·01	1·95	—	1·68
Striatella sp. non det.	—	—	—	0·08	—	—
Navicula membranacea	—	0·03	—	—	—	—
Navicula spp. non det.	0·04	0·17	1·18	0·06	—	—
Pleurosigma capense	0·01	0·01	—	—	—	—
Pleurosigma sp. non det.	0·02	—	—	—	—	—
Nitzschia closterium	0·81	—	2·37	0·23	11·80	0·78
N. delicatissima	0·31	8·24	17·96	16·96	55·04	19·36
N. longissima	0·06	—	—	0·52	—	—
N. seriata	21·77	31·11	9·40	45·43	1·92	39·73

The cosmopolitan distribution of marine plankton diatoms and the 'ecological' characterization' of the more important species from the Benguela current

A further selection of the most important or typical diatom species observed within the area permits concise illustration of the extremely cosmopolitan distribution of these in other regions, so that it is the relative importance of the various forms rather than their mere presence and absence that must be studied before relationships between the floras and their 'conditions of existence' begin to be perceptible. This further selection has been used to give examples of the brief 'ecological characterizations' of species, on Gran's lines, that are so helpful in the attempt to perceive some order in the ever-changing phytoplankton communities.

Table 28 shows reported occurrences of these typical Benguela current species in various other regions, ranging from the North Atlantic to the antarctic zone of the southern ocean. Some of these have received much less complete coverage than others, and yet other regions might be added, especially around Japan (cf. Aikawa, 1936), but the table is surely adequate to show the very cosmopolitan distribution of most of the species. This fact was generally recognized by most of the earlier phytoplankton workers (cf. Gran and Braarud, 1935, and Aikawa 1936, among others), but it probably became so obvious to them that they rarely sought to stress it. The species listed in Table 28 are selected on the ground that we have observed them to be dominant, typical or otherwise important in the Benguela current, and without reference to their occurrence elsewhere. But there is no reason to suppose that the less important or typical species—except perhaps the neritic ones (see below)—are any more restricted in their distribution. At least it can be said that of all the eighty-two species identified from the Benguela area so far, none are 'new to science'.

The supreme importance of the inshore chaetocerids (of the group Hyalochaete) in the upwelling regions, can only be fully appreciated when quantitative data are considered, but is still apparent here in the relatively large number of species recorded. It can also be seen that the holoplanktonic, mainly oceanic solenoids are perhaps the most completely cosmopolitan of all plankton diatoms, though panthalassic 'reversionary plankton forms' such as *Nitzschia seriata* are almost equally widely distributed.

The few important species that seem to be limited to the Benguela current area and adjacent South African coasts are all inshore ones: *Chaetoceros strictum* and *C. tetras*, *Fragilaria granulata* and *F. karsteni*. Certain other coastal species are recorded from comparatively few of the other regions mentioned, but since these include major upwelling regions their very widespread distribution is in no doubt. Further sampling will almost certainly reveal their presence in the less favourable intervening areas eventually, though probably in such small numbers as to form but an insignificant proportion of the sparse populations to be found there. These forms include *C. costatum*, recorded elsewhere from the coast of southern Europe and North Africa, California and Japan; *C. pseudocrinitum*, S. temperate coasts of Europe and California, and *C. van heurckii*, recorded only from California and the Madras coast of India among the other localities considered. *Nitzschia longissima* also has a comparatively restricted occurrence, so far as it is yet known, being recorded only from the other African localities, California and Japan.

Proceeding to brief 'ecological characterizations' of the several species on the basis of our observations in the Benguela current area, it is necessary to make the proviso that maximal occurrence during spring or autumn may indicate *either* a normal seasonal effect *or* merely that these species tend to flourish earlier or later in a succession that quite probably repeats itself several times in the course of a year, as the more or less persistent upwelling system waxes and wanes.

Table 28. *Distribution in other regions, defined below (with sources).* × *positive records*

Selected abundant or typical Benguela current species	*South African waters*			*North and Tropical Atlantic*				*Indian Ocean*	*West Pacific*		*East Pacific*		*Southern Ocean*	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
DISCINEAE														
Stephanopyxis turris	×	×	×	×	—	×	×	×	—	—	×	×	×	×
Thalassiosira subtilis	×	—	×	×	—	×	×	×	×	×	×	×	×	×
Planktoniella sol	×	×	×	×	—	×	×	×	×	×	×	×	×	×
BIDDULPHIACEAE														
Biddulphia longicruris	×	—	—	—	—	—	×	×	—	—	×	×	—	—
Eucampia zoodiacus	×	—	×	×	×	×	—	×	—	×	×	×	—	—
CHAETOCERACEAE														
Chaetoceros affine	—	×	×	×	×	×	×	×	×	×	×	×	—	×
C. atlanticum+var. *neapolitanum*	××	—	××	××	×—	××	——	——	××	××	××	——	×—	×—
C. compressum	—	—	×	×	×	×	—	×	×	×	×	—	×	—
C. constrictum	×	×	×	×	×	×	—	—	—	—	×	—	—	—
C. convolutum	×	—	—	×	×	×	—	—	—	—	×	—	×	×
C. costatum	—	×	—	×	—	×	—	—	—	×	×	—	—	—
C. curvisetum	×	—	—	×	—	×	—	×	—	×	×	×	—	—
C. debile	—	×	—	×	×	×	—	—	×	×	×	—	×	—
C. decipiens	—	—	×	×	×	×	×	—	×	×	×	—	×	×
C. didymum	×	×	×	×	×	×	×	×	—	×	×	×	×	×
C. difficile	×	×	—	×	—	—	—	—	—	×	×	—	×	—
C. laciniosum	—	—	—	×	×	×	—	×	—	×	×	—	—	×
C. lorenzianum	×	×	—	×	—	×	×	×	×	×	×	×	×	×
C. peruvianum	×	×	×	—	—	×	×	×	—	×	×	×	×	×
C. pseudocrinitum	—	—	×	×	×	—	—	—	—	—	×	—	—	—
C. sociale	×	×	—	×	×	—	×	×	—	×	×	×	×	×
C. strictum	×	×	—	—	—	—	—	—	—	—	—	—	—	—
C. subsecundum	×	—	—	×	×	×	—	—	—	—	×	—	—	×
C. teres	×	—	—	×	×	×	—	—	—	×	×	—	—	—
C. tetras	×	×	—	—	—	—	—	—	—	—	—	—	—	—
C. van heurckii	×	—	—	—	—	—	—	×	—	—	×	—	—	—
SOLENIINEAE														
Rhizolenia alata	×	×	×	×	×	×	×	×	×	×	×	×	×	×
R. hebetata	×	×	—	×	×	×	×	×	×	×	×	×	×	×
R. imbricata	×	×	×	×	×	×	×	×	—	×	×	×	×	×
R. setigera	—	—	—	×	×	×	×	×	×	×	×	—	—	—
R. styliformis	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Leptocylindrus danicus	×	—	×	×	×	×	—	×	×	×	×	×	—	—
Dactyliosolen mediterraneus	—	—	×	×	×	×	—	—	—	×	×	—	—	—
Corethron criophilum	×	×	×	×	×	×	×	×	×	×	×	×	×	×
PENNATAE														
Fragilaria granulata	×	—	×	—	—	—	×	—	—	—	—	—	—	—
F. karsteni	×	×	—	—	—	—	—	—	—	—	—	—	—	—
Asterionella japonica	×	—	×	×	×	×	×	×	×	×	×	—	×	—
Thalassionema nitzschioides	×	×	×	×	×	×	×	×	—	×	×	×	×	×
Thalassiothrix longissima	×	—	×	×	×	×	×	×	×	×	×	×	×	×
Nitzschia closterium	×	×	—	×	×	×	×	×	—	×	×	—	×	×
N. delicatissima	×	—	—	×	×	×	—	—	—	×	×	—	×	×
N. longissima	×	—	—	—	—	—	×	×	—	×	×	—	—	—
N. seriata	×	×	×	×	×	×	×	×	×	×	×	×	×	×

1 Atlantic coast of Cape Province (Boden, 1950).
2 Between Cape Town and Port Elizabeth (Karsten, 1906).
3 Agulhas current (Hendey, 1937).
4 'Northern Seas' (Lebour, 1930).
5 Bay of Fundy, Gran and Braarud, 1935.
6 Temperate and subtropical North Atlantic, including Canary current (K. R. Gaarder, 1951).
7 Tropical Atlantic (Karsten, 1906, and others).
8 Madras coast of India (Subrahmanyan, 1946).
9 Chu San I. China, *ca.* 30° N. lat. (Sproston, 1949).
10 Pacific coast of Japan (Aikawa, 1936; Marumo, 1954; Takano, 1954).
11 Pacific coast of North America, including California current (Cupp, 1943; Sleggs, 1927; Allen, 1938).
12 Peru current (Hendey, 1937).
13 Subantarctic, mainly Atlantic sector (Hart, 1934; Hendey, 1937).
14 Antarctic (Hart, 1934, 1942; Hendey, 1937).

Stephanophyxis turris was here an inshore ('coastal' or 'neritic') species found mainly in the northern (warmer) part of the area surveyed. Much more abundant in autumn than during spring.

Thalassiosira subtilis had a panthalassic distribution. Maximal abundance inshore in autumn; greatest relative importance offshore during the spring survey.

Planktoniella sol. An oceanic species relatively important at sparsely populated offshore stations only, during both surveys.

Biddulphia longicruris. An inshore species frequent and 'typical' though never abundant, in spring samples; not yet observed at all in autumn ones at the dilutions necessary to obtain counts.

Eucampia zoodiacus. An inshore species with precisely the converse of the seasonal distribution of *Biddulphia longicruris. Eucampia zoodiacus* was not seen at all during analysis of the spring samples. In autumn it was abundant, sometimes one of the dominant species close inshore.

Chaetoceros atlanticum (type) mainly offshore with pronounced spring maximum.

Chaetoceros atlanticum var. *neapolitanum* even more definitely restricted to offshore waters than the type (with relatively high temperature) but also in some of the same samples.

Chaetoceros affine (syn. *C. Ralfsii*) here a strongly neritic species much more abundant in autumn than during spring.

Chaetoceros compressum was one of the most abundant species at both seasons inshore, but sufficiently panthalassic for the 'overspill' to dominate at a few of the sparser offshore catches as well.

Chaetoceros constrictum. Very important during both surveys. Distributed much like *C. compressum.*

Chaetoceros convolutum was mainly an offshore species most abundant during spring.

Chaetoceros costatum, an inshore species most numerous in autumn (or late in the succession).

Chaetoceros curvisetum, mainly inshore and with a spring maximum, but very important at both seasons. The most abundant species in these samples. Showed sufficient panthalassic tendency to dominate some offshore samples as well, like *C. compressum* and *C. constrictum,* which often occurred with it.

Chaetoceros debile. Inshore, most in autumn, very local here.

Chaetoceros decipiens. Panthalassic, though mainly offshore here, more in spring than in autumn.

Chaetoceros didymum. An inshore species with pronounced autumnal maximum, when the resting spores were even more abundant than the vegetative phase.

Chaetoceros difficile. Mainly inshore with autumn maximum.

Chaetoceros laciniosum. An inshore species, local here, with strong spring maximum.

Chaetoceros lorenzianum. Panthalassic here with spring maximum far offshore at the outer end of the Orange river line.

Chaetoceros peruvianum. Offshore form more abundant during spring than in autumn.

Chaetoceros pseudocrinitum. An inshore or shelf species here, most in autumn.

Chaetoceros sociale. A panthalassic species on its showing here, abundant at some very localized inshore stations, but relatively more important offshore in spring.

Chaetoceros strictum. An inshore species observed most abundantly during the spring survey.

Chaetoceros subsecundum. An inshore species with autumn maximum, when many of the characteristic resting spores were present.

Chaetoceros teres. An inshore species most abundant in autumn here.

Chaetoceros tetras. A very local species abundant at a few inshore stations, most in spring.

Chaetoceros van heurckii. An inshore species most abundant in autumn.

Rhizosolenia alata. Panthalassic rather than exclusively oceanic here, most important offshore in spring, but numerous during both surveys.

Rhizosolenia hebetata. Present here almost exclusively in the form (or phase) *semispina.* Was most numerous inshore in spring, but of much greater relative importance offshore, especially in autumn. Panthalassic seems a fairer description than oceanic for this extremely cosmopolitan form.

Rhizosolenia imbricata. Here var. *Shrubsolei* was more frequent than the type, but both were present in the same samples at times. Panthalassic, reaching its greatest relative importance offshore at both seasons.

Rhizosolenia setigera. An inshore form with spring maximum.

Rhizosolenia styliformis. Panthalassic, but mainly offshore with a pronounced spring maximum.

Leptocylindrus danicus. An inshore species most abundant in autumn.

Dactyliosolen mediterraneus. Panthalassic, maximum inshore in autumn, but offshore during the spring survey!? Stenothermal.

Corethron criophilum. Panthalassic here, where most were seen inshore or on the outer shelf in spring. Of its generally oceanic character in most phases there can be no doubt.

Fragilaria granulata. Panthalassic? Recorded here only from the outer shelf or even offshore, never overlapping with the next species. Not recorded elsewhere except off South Africa.

Fragilaria Karsteni. Very definitely neritic and with a spring maximum, but also quite abundant during the autumn survey. Recorded elsewhere only off Cape Province (Karsten (syn. *F. capensis*) Boden).

Asterionella japonica. An important inshore and outer-shelf species, especially in autumn when it was one of the few other species to rival the dominant chaetocerids in abundance, and partly responsible for visible discoloration of the water at some stations close inshore.

Thalassiothrix longissima, though never very abundant, was relatively important offshore at both seasons, rather more so in spring than during the autumn survey.

Thalassionema nitzschioides. An inshore species, very local in this area, chiefly in spring (or early in the succession).

Nitzschia closterium. Tychopelagic, a littoral species fairly frequent in plankton close inshore, but never abundant here.

Nitzschia delicatissima. Panthalassic, mainly offshore with an autumn maximum here.

Nitzschia longissima. Never abundant, but very characteristic of the inshore plankton here, especially on the spring survey. Possibly littoral, tychopelagic.

Nitzschia seriata. Panthalassic, abundant and important at both seasons studied. Most important offshore in spring, but more abundant inshore.

Comparing these ecological notes with those of other workers, principally Gran, Lebour, Braarud and Gran, Cupp and K. R. Gaarder, as referred to in the sources of Table 28, it appears that a large majority of the species considered important or typical in the Benguela area were disposed therein just as one would expect from their recorded distributions elsewhere. Minor modifications of previous ecological characterizations based on these results, and on earlier work in the southern ocean (Hart 1934, 1942), are suggested as follows:

Thalassiosira subtilis should probably be regarded as panthalassic rather than oceanic. Though cosmopolitan in the open oceans, it frequently attains greater abundance near land. Gaarder's (1951) note that though widespread in the Michael Sars material from the North Atlantic, the species was observed most abundantly close in to the Azores, accords with this view.

Conversely several of the dominant chaetocerids of the rich inshore waters, though undoubtedly neritic in the main as recorded elsewhere, showed a more or less pronounced panthalassic trend; since lesser numbers of them flourished sufficiently far offshore to dominate the sparser communities encountered there. This trend was most marked in *Chaetoceros Lorenzianum*, but was also shown by the three most abundant of all the diatoms met with: *C. compressum*, *C. constrictum* and *C. curvisetum*.

The inshore or neritic species *C. subsecundum* exhibited a striking seasonal difference from its known disposition in the northern hemisphere, where most observers have recorded a strong maximum in spring or early summer. On our two surveys it was relatively much more abundant in autumn. Possibly we missed an earlier maximum through lack of full seasonal coverage, which would show up any repetition of the succession at a shorter interval of time. Equally we may here have a real difference due to the 'conditions of existence', biological as well as physical. In the northern hemisphere the species has been regarded as arctic-boreal or boreal, but both Gaarder's results and our own show that it can flourish in much warmer temperate waters than the earlier records suggest, where it must find itself among a very different and much more varied phytoplankton community.

The holoplanktonic cosmopolitan solenoids: *Rhizosolenia alata* and *R. hebetata. f. semispina* would seem definitely better described as panthalassic rather than oceanic. Their dominance at certain sparsely populated oceanic stations is unquestioned, but at the same time they were often found in greater numbers among the rich *Chaetoceros* plankton close inshore. The same applies in a less marked degree to *R. imbricata* (mainly the variety *Shrubsolei*; the larger type phase was rarer and 'more

oceanic' here, though they occasionally occurred in the same samples). Temperature is probably the factor involved, having regard to the distributional records of the two forms elsewhere (cf. p. 217).

Similarly *Corethron criophilum* and even the well-known *Rhizosolenia styliformis* both tended to display a more panthalassic trend than their usual designation as oceanic forms would lead one to expect. In support we may cite the abundant occurrence of *Corethron* (in some of its phases) close in to the land as well as offshore in the antarctic zone of the southern ocean, and the occurrence of almost pure communities of *Rhizosolenia styliformis* in the shallow waters of the North Sea (Hardy, 1923; Wimpenny, 1936).

Concerning *Dactyliosolen mediterraneus* previous opinions were 'neritic' (Lebour) and 'neritic, sporadically oceanic'. K. R. Gaarder (1951) found moderate numbers of it in samples from all over the area covered by the 'Michael Sars' to the west and south of the British Isles. In the Benguela material the species was locally abundant offshore in spring and inshore in autumn, suggesting that it thrives only within narrow limits of temperature (stenothermal, with optimum range about 15° to 19° C.). Certainly 'panthalassic' would seem to be the best brief description of its general distributional trend.

Finally, two of the most abundant 'pennatae', *Nitzschia delicatissima* and *N. seriata*, previous ecological descriptions of which range from 'perhaps oceanic, but often abundant inshore', to definitely 'neritic', would in the opinion of the writer (T.J.H.) be better described as panthalassic—expressing the duality of the best of the earlier descriptions in one word. They were numerous in both inshore and offshore samples in the area studied here, and also in antarctic seas (Hart, 1934, 1942).

These minor differences from previous brief ecological descriptions of the species are so few that it is the general concordance with the opinions of those with the greatest experience of working through large collections of material that is striking, encouraging the belief that in this direction at least plankton workers grope towards 'the truth' to some purpose. Although Gran's 'system of plankton elements' must necessarily be modified as data from the less-known sea-areas becomes available, the ideas implicit therein remain one of our greatest aids in the attempt to understand the relations between phytoplankton communities and their 'conditions of existence'.

This comparison of the diatom-flora of the Benguela current with those of other regions brings out one important point, implicit in much that has been published already, but little emphasized by the earlier authors: that there is a fundamental difference between the diatoms and, for example, the species of oceanic zooplankton, in the nature of their distribution.

Although there are some cosmopolitan species of zooplankton, the range of the majority is subject to some limit beyond which they are unknown. Where there is a region offering an environment similar to that occupied by such a species, but isolated from it, we normally find there a similar species, but a distinct one. Most of the plankton diatom species, however, excepting certain neritic, polar, or markedly stenothermal warm-water forms, are not limited in their dispersal by 'barriers' to anything like the same extent as the zooplankton. Many of the more cosmopolitan diatoms may turn up almost anywhere in the oceans of the world, and become locally important or even dominant, wherever the 'conditions of existence' best suit them.

It is for this reason that the plankton floras of adjacent water masses must be studied with more regard to the differing proportions of the various species within them, than to the presence or absence of particular forms.

ZOOPLANKTON

On both of the 'William Scoresby's' surveys net hauls were made to sample the zooplankton. Full particulars are given in the Station List (1953). On survey I these consisted of a series of vertical hauls with the 'Discovery' N 70 V net, and were taken only on the three main latitudinal lines of stations. On survey II the hauls were extended to include a surface haul with a metre stramin net (N 100 H) at all stations and in addition an oblique haul with a metre stramin and 70 cm. net (N 100 B, N 70 B) was made at all 'full stations'—that is, again on the latitudinal lines of stations.

One of us (T.J.H.) has sorted the zooplankton hauls from survey I, and the material has so far as possible been distributed to specialists in the various groups. Reports on some groups have already been published, and we present a synopsis of the findings of these. Where it has not yet been possible to find specialists to work up the groups, they have been provisionally identified and the results are used in the following general account, sometimes merely to give a picture of the distribution of the group as a whole. Some important groups, notably the Copepoda, have not yet been dealt with.

The zooplankton samples from survey II have not yet been sorted, apart from some groups—fish eggs and larvae, Cumacea and Chaetognatha—whose distribution had proved unusually interesting during the first survey. These results are included in the following account.

Polychaeta

Most of the polychaets in the collection were larval or juvenile forms. These have not yet been examined in detail and it is hoped that they will be dealt with separately at a later date. It is interesting to note, however, that some seemed to show a tendency towards a prolonged post-larval sojourn in the plankton over the regions where the bottom waters were exceptionally deficient in oxygen.

Chaetognatha

The chaetognaths in the collection from survey I have been examined and identified by Mr P. M. David, and will be dealt with in a separate report by him. The following notes have been made from the figures kindly supplied by Mr David.

The distribution of the species seems to follow a rather similar pattern on all three lines of stations. Close to the coast in the surface-layers *Sagitta friderici* Ritter-Zahony was dominant. Immediately seawards of this, *S. serratodentata* Krohn became the dominant species, still, however, in the shallower waters of the continental shelf, although this latter species was also found in smaller numbers at the oceanic stations WS 977 and 996. *S. decipiens* (Fowler) occupied a position just off the edge of the continental shelf and generally somewhat deeper in the water column, the main centre of abundance varying from line to line in depths of about 100–400 m.

Eukrohnia hamata (Mobius) was concentrated mainly farther seawards than the *Sagitta decipiens*, in the deeper layers, while above the *Eukrohnia hamata* population, varying numbers of *Sagitta minima* (Conant) and *S. lyra* (Krohn) were taken. Some numbers of *S. lyra* were also taken at station WS 978.

Entomostraca

Dr J. P. Harding has very kindly confirmed the identification of the specimens of Cladocera which were picked out from the samples. Both *Evadne nordmani* Lovén and *Podon polyphemoides* Leuck. were present in the collections, and *Evadne nordmani* was the relatively more abundant species.

The Cladocera were present only at the stations lying close to the coast. Off Walvis Bay at WS 981, they reached their greatest concentration, more than 600 *Podon polyphemoides* and nearly 2200 *Evadne*

nordmani being present in the 50–0 m. haul. At the next station seawards, WS 980, they were only present in the 50–0 m. haul (one *Podon polyphemoides* and twenty *Evadne nordmani*), the 100–50 m. haul and all other hauls on this line of stations being devoid of Cladocera.

On the Sylvia Hill line only two *E. nordmani* were taken at the station closest to the coast (WS 989), and although no specimens were taken on the Orange river line, one specimen of *E. nordmani* was recorded farther south at WS 1043 on the second survey.

It was very noticeable during sorting how completely the Ostracoda gave way to Cladocera close in to the land on each line of stations. Here it seems that the marine ostracods constitute an essentially oceanic mid-water group, while the Cladocera were confined to the most neritic part of the coastal current. The two groups showed an almost complete absence of overlap in the first survey samples.

Ostracoda

Mr E. J. Iles (1953) has published a report on the ostracods in the collection. Nearly all of these occurred at the offshore stations. As with the mysids, variety rather than numerical abundance characterized the group. Three genera were present, and of one of these, *Conchoecia*, twenty-three species occurred in the samples.

Four or five species of *Conchoecia* predominated, but by far the greatest number were contributed by the species *Conchoecia elegans* Sars.

C. elegans mainly inhabited the 500–250 m. layer off the edge of the continental shelf on the three main lines of stations, but there are also indications that it shows a vertical migration, similar to that described by Fowler (1909) in the Bay of Biscay, and more than eighty adults were found in the 50–0 m. layer at the night station WS 977.

C. nasotuberculata Müller, and *C. curta* Lubbock, both appeared to occupy a depth distribution similar to that of *C. elegans*, or perhaps at rather shallower levels. *C. alata* Müller was found at greater depths, 500 m. or more, while *C. symmetrica* Müller was amongst the deepest species of all, possibly even exceeding 1000 m., the greatest depth of the net hauls.

C. teretivalvata Iles occurred in quite large numbers in the shallower layers, i.e. in samples from 250–100 m., except at one station, WS 976, where an anomalous haul of twenty-four specimens occurred in the 750–500 m. layer.

As previously noted the ostracods did not overlap the Cladocera, and indeed at the inshore stations their niche appears to be filled by the latter group.

Mysidacea

Dr Tattersall (1955) has examined and reported on the collections of mysids,[1] and the following remarks are abstracted from her report.

Only at one station, WS 1002, were large numbers of individuals taken. Here, in the 50–0 m. haul, there were over 450 specimens of the gregarious mysid, *Gastrosaccus sanctus* (van Beneden). One small juvenile specimen of the same species was taken rather farther seaward at station WS 1000. Both these stations are somewhat farther south than is normally recorded for this species.

In spite of the paucity of numbers in the net hauls at the other stations, there was a richness of species in which ten genera and sixteen species were recorded. Many of these occur within the known geographical range of the species. *Boreomysis rostrata* Illig occurred in the deeper 750–500 m. hauls at the offshore stations. Two species, however, show an interesting deviation from their normal range. *Dactylamblyops hodgsoni* Holt and Tattersall has previously been recorded only from deep waters in

[1] Her report is on a much larger collection which includes those from the Benguela current.

the Southern Ocean, and at station WS 976 one juvenile specimen was taken in the 1000–750 m. haul. The other species, *Euchaetomera zurstrasseni* (Illig), although originally recorded from the Indian Ocean west of the Chagos Islands, has only been recorded once in the waters to the west of Cape Town, and is usually only taken in the far south of the Atlantic Ocean. One specimen occurred at station WS 976.

Cumacea

The Cumacea were identified by Dr N. S. Jones and the following account has been abstracted from his report on the group (1955).

Four genera and five species were present in the samples, but only the genus *Iphinoe* attained considerable numerical importance. This is not altogether surprising, for the Cumacea are normally bottom-living forms, but the appearance of one species (*Iphinoe fagei*, Jones) in considerable numbers in the plankton—exceeding 7000 in one haul at station WS 989—is of great interest.

The collections of Cumacea are confined to the stations relatively close to the coast, in shallow water. Evidently there is a succession of species from north to south. *Bodotria glabra* Jones occurred only in small numbers and only on the most northerly line of stations (19° 44′ S). On both the Walvis Bay line and Sylvia Hill line the two species of *Iphinoe*, *I. africana* Zimmer and *I. fagei*, were dominant in abundance. *Upselaspis caparti* (Fage) was present only off Walvis Bay and *Diastylis rufescens* Jones occurred only on the Orange river line.

The large catches of Cumacea occurred in the night hauls at stations WS 988 and 989, and *I. fagei* was the most abundant species. Jones notes that 'although the species present in these hauls may be able to live normally in the plankton, they show no special adaptations to this mode of life and their nearest relatives are coastal bottom-living forms'. Further, he says that when Cumacea have been caught in tow-nets at night, adult males have usually predominated, especially when attracted by artificial light, although in some recent records newly moulted adult or ovigerous females have outnumbered the males. In the hauls containing the largest numbers of specimens described here, both males and females of all stages were represented. These could possibly have been a nuptial swarm, but the following is a rather attractive alternative explanation.

It is interesting to compare these catches with a sample of the bottom fauna taken near Walvis Bay by Professor Spärk (1953). Here, in the belt of sand inside the anaerobic zone (p. 204), Spärk took 1910 Cumacea in a Petterson grab sample. Both stations WS 988 and 989 lay over the anaerobic zone, and if Spärk's specimens were the same species, *Iphinoe fagei*, then it seems reasonable to suppose that the great development of the anaerobic zone in March may have forced the Cumaceans up from their usual habitat on the sea-bed, to adopt a planktonic existence in the waters nearer the surface where oxygen would have been available.

The numbers of *Iphinoe* sp. corresponded closely with the distribution of the pilchard eggs and larvae (see p. 272).

Amphipoda

Although the amphipods have been separated from the samples, they have not been identified further, and it is only possible to remark on the total abundance of the group. They were present in relatively small numbers at all of the stations except WS 981. Their greatest abundance was at the offshore stations, where at WS 986, over 270, which appear to be mainly juvenile *Vibilia* sp., occurred in the 50–0 m. haul, but they were also present in moderate numbers at the inshore stations on the Orange river line. These *Vibilia* sp. appeared in numbers at stations where salps were also abundant, as was to be expected from the known commensalism between these animals.

Euphausiacea

Boden (1955) notes that fourteen species of euphausiids were represented in the collection from survey I. The numbers of adult euphausiids were quite small, but larvae of some species were numerous in some of the catches.

Nyctiphanes capensis Hansen was only taken at the stations on the continental shelf—excepting one larva which occurred in the 1000–750 m. haul at WS 997. It was present on all three latitudinal lines of stations. On the Orange river line the larvae extended farther seawards than the adults, but on the Walvis Bay line the greatest abundance of larvae—totalling 5000 specimens—occurred at WS 979, and this coincided with the greatest number of adults (twenty-seven) on this line.

The adults of *Euphausia lucens* Hansen, an oceanic species, occurred in very small numbers at the offshore stations, but a large haul of 237 adult females was taken in the 50–0 m. layer at WS 1000 on the continental shelf, and the adults were also present off the Orange river mouth (WS 1001 and WS 1002). The larvae were mainly abundant at the offshore station on the Orange river line (WS 996), but Barry (1956) in comparing Boden's material with some from New Zealand, questions the identification of these larvae as *E. lucens* and considers they may belong to some other species.

E. tenera Hansen, a tropical to subtropical form, occurred only at WS 996, at the offshore end of the Orange river line. Most larvae of this species were in the 250–100 m. haul. Boden is of the opinion that many of the unidentified pre-furcilia larvae encountered at other stations may in fact be *E. tenera*.

E. recurva Hansen, which occurred offshore on the Walvis Bay and Orange river lines, shows some suggestion of diurnal migration. *E. hanseni* Zimmer was represented by four adults in the 250–100 m. layer at stations WS 978 and 987 just off the continental shelf.

Of *Nematoscelis megalops* G. O. Sars mostly larvae were taken at the oceanic stations, and these, concentrated at about 250 m. during the day, show a diurnal vertical migration.

A species usually common in this area, *Thysanoessa gregaria* G. O. Sars, was present in very small numbers, well offshore.

Four species of *Stylocheiron* were also recorded.

Decapoda and Stomatopoda

The collections of survey I have been examined and described by Dr M. V. Lebour (1954). Nearly all of the material consists of larval stages, but a few species are represented in adult form. A large number of genera and species were represented, but few were present in any abundance and the small number of individuals does not warrant a detailed account of their distribution.

Callianassa larvae were present at the inshore stations at Walvis Bay and on the continental shelf on the Orange river line. The phyllosoma larvae of *Jasus lalandii* (Lamark), the common crawfish of South Africa, were represented only by two specimens taken at stations WS 992 and 1000.

Among the Brachyuran larvae, a species of *Ebalia* occurred at both the offshore and shelf stations on the Orange river line.

Five adult specimens of the stomatopod, *Squilla armata* Milne-Edwards, were taken in a trawl in 128 m. of water at WS 990. Larvae of the same species occurred in ones or twos at the three inshore stations off Orange river mouth.

Mollusca

The collections of planktonic molluscs have been reported on by Dr J. E. Morton (1954).

Specimens of the surface-living gastropod, *Ianthina ianthina* (Linnaeus) and *I. globosa* Swainson were taken by hand nets at two offshore stations (WS 1057 and 1058) on survey II. The heteropod,

Atlanta peroni Lesueur, a species common in subtropical Atlantic waters, occurred in small numbers at the offshore station on the Orange river line on survey I.

The pteropod *Limacina* was, however, numerically the most abundant mollusc in the collections. Two species occurred, the first *L. inflata* (d'Orbigny) only in small numbers at the offshore station WS 986. The other species *L. bulimoides* (d'Orbigny) also occurred at the same position, but was principally found at the offshore stations on the Orange river line. Here it reached great concentrations at the two stations WS 996 and 997. More than 3000 individuals were taken in the 250–100 m. haul at station WS 997.

We have seen (p. 229) that there was evidence of heavy grazing of the phytoplankton at these two stations and this may well be attributed to these enormous numbers of pteropods. Also present at these two stations were some specimens of the gymnosomatous pteropod, *Pneumodermopsis paucidens* Boas and its close association with the *Limacina bulimoides* and its probable feeding habits suggest that it may have been preying upon the *L. bulimoides*.

Two species of lamellibranch larvae occurred in the collections. Five hundred and forty individuals of larva 'A' were taken in the 50–0 m. haul at station WS 981 off Walvis Bay. The other species, larva 'B' was present off Sylvia Hill at stations WS 988 and 989 and more numerously off the Orange river mouth where 600 were taken at station WS 1002.

Larvacea

The appendicularia from the samples, which include the genera *Oikopleura* and *Fritillaria*, have not yet been identified, but some remarks may be made on the distribution of the group as a whole.

Very large numbers occurred at the three inshore stations on the Walvis Bay line (WS 979, 980 and 981) reaching a maximum of about 5400 in the 50–0 m. haul at WS 980. The numbers fell off sharply, however, and only five individuals were present between 500 m. and 100 m. at station WS 978. At the stations seaward of this, modest numbers occurred in the surface-layers.

On the Sylvia Hill line of stations, a reversal of these conditions was observed. At the outermost station, WS 986, fairly large numbers occurred in all of the hauls. At WS 987 none of the hauls contained appendicularia. At station WS 988, large numbers ($>$ 200) were again encountered in both the 50–0 m. and 100–50 m. hauls and at the station nearest the coast numbers decreased once more.

This distribution was nearly paralleled on the Orange river line, where virtually all of the appendicularia occurred at the two offshore stations. None was present inshore at stations WS 1000, 1001 and 1002. At the offshore stations numbers were highest in the surface-layers, and decreased with depth.

The explanation of this distribution is not easy without a more specific identification of the individuals. It may conceivably be the result of the presence of two separate populations of appendicularia —the first, in abundance inshore at Walvis Bay and extending southwards to WS 988 and 989 at the inshore end of the Sylvia Hill line, and the second, offshore on the Orange river line and Sylvia Hill line (WS 986) and extending northwards in decreasing numbers to the offshore end of the Walvis Bay line. Confirmation of this suggestion, will, however, have to await a more detailed examination of the species.

Eggs and young stages of fish

Hart and Marshall (1951) have already commented on the fish-eggs and larvae which occurred in the plankton hauls. Of particular interest were the large numbers of eggs and larvae of *Sardinops sagax ocellata*, which occurred at the inshore end of all of the lines of stations, but particularly at the inshore stations on the Walvis Bay and Sylvia Hill lines. The greatest catch of 1000 eggs was taken in the

50–0 m. haul at station WS 989. Evidently spawning took place within 25 miles of the coast, in depths of about 50–150 m. A few post-larvae were taken in the deeper net hauls, but all were confined to the waters on the continental shelf. The heaviest catches occurred where the mean temperature of the upper 50 m. of the water column lay between 13° and 14·5° C. The importance of locating a spawning ground of this, the South African pilchard, is referred to on p. 270.

The eggs and young stages of other fish were also taken, notably those of the stockfish (*Merluccius capensis*), and of anchovies (*Engraulis* sp).

Distribution of the zooplankton

From the foregoing notes it is evident that there are many characteristic features in the zooplankton distribution, several of which might be expected from the known behaviour of the organisms. The ostracods, for example, are in this region an essentially mid-water group, lying off the edge of the continental shelf and showing a fairly well-defined distribution of species with depth, *Conchoecia elegans* being the dominant species and occupying the 500–250 m. layer. In the shallower waters, the role of the ostracods appears to be taken over by the Cladocera, which locally reached great abundance inshore on the Walvis Bay line.

The mysids were, on the whole, very poorly represented numerically, and only the one species, *Gastrosaccus sanctus*, which is normally particularly gregarious, attained any considerable numbers. This concentration occurred in the rather diluted water off the Orange river mouth. On the more northerly lines very few specimens were taken, and it is interesting to compare this with the abundance of cumacea at these more northerly stations.

The dominant cumacean, *Iphinoë fagei*, is closely related to other bottom living forms, and shows no particular adaptations to a planktonic existence. The large numbers occurring planktonically inshore on the Sylvia Hill line may be explained as being a nuptial swarm. But when one considers other phenomena—such as the presence of larval tubicolous polychaets with their tubes partly developed, the larval lamellibranchs with shells developed, and the post-larval Ophiuroids, all in the plankton—then one is more inclined to accept the alternative explanation, that the sea-bed of the anaerobic zone did not present a desirable environment and forced into the plankton many organisms which would otherwise have been present on the sea-bed at these stations.

The presence of the euphausiid *Nyctiphanes capensis* on the continental shelf is quite characteristic of its habit, and the other euphausiid, *Euphausia lucens*, only reached large numbers in the vicinity of the Orange river mouth, again in the shallow coastal waters. The close similarity in succession of species between the euphausiid fauna of this region, and that found off California, described by Boden, seems significant in view of the hydrological similarities between the two regions.

At the offshore end of the Orange river line the large numbers of the pteropod *Limacina bulimoides*, evidently grazing heavily on the phytoplankton (p. 229) and probably being preyed upon in turn by the gymnosomatous pteropod *Pneumodermopsis paucidens*, is the only major occurrence of the pelagic molluscs in the collection.

The distribution of the Larvaceae is strongly indicative of the presence of two separate populations, one in the coastal waters to the north, and the other in the oceanic waters to the south.

The association between the young amphipods (*Vibilia* sp.) and the salps, both of which occurred in numbers at the offshore end of the Sylvia Hill line, is no doubt an example of the well-known commensalism between these animals.

The correlation between the numbers of cumacea and the numbers of eggs and young stages of the pilchard is probably purely coincidental, but may be of some value since the cumaceans are fairly large and easily seen, and could perhaps be used as an 'indicator' for the pilchard eggs.

Taking the zooplankton as a whole, one gets the impression of a rather patchy and spasmodic distribution, quite large numbers of individuals of particular species occurring rather locally. This impression must, of course, be contributed to very largely by the fact that a relatively small number of stations cover a rather large area, but nevertheless there are few occurrences which suggest the population of specific water masses by particular organisms. The picture formed, in contrast to that created by the phytoplankton, rather suggests an independence from the more particular water masses, and an occupation by the animals of ecological niches more suited to their own habit than conforming to the circulation of the water masses. This applies in particular to the chaetognaths, whose distribution follows a similar pattern on all three lines of stations—*Sagitta friderici* occupying the water near the coast, with *S. serratodentata* a little farther offshore, and *S. decipiens* in the deeper water at the very edge of the continental shelf.

ECONOMIC RESOURCES OF THE BENGUELA CURRENT

Fish and fisheries

In a region so organically rich as the Benguela current it is only to be expected that animals higher in the food chains and of more direct interest to man should also be found in abundance. In fact the pelagic fishes are already being increasingly exploited and among them the South African pilchard takes first place as the basis of extensive fisheries at various points along the coast. Following closely in importance are fisheries for the 'maasbanker' (*Trachurus trachurus*), stockfish (*Merluccius capensis*) and snoek (*Thyrsites atun*), and many sharks are taken principally for their liver oil.

It is clearly impossible, in a brief oceanographical survey, to obtain more than a glimpse of the fish populations and any account of these is more in the ambit of the Fisheries Division of the Department of Commerce and Industries in the Union of South Africa, which is conducting extensive research on this problem.

However, the inclusion of regional plankton sampling as part of the survey did reveal one point of major significance to the economic development of the region, and that is the discovery of an extensive spawning ground of the South African pilchard. As stated on p. 272 evidence was found of great concentrations of eggs and larvae near the coast in the vicinity of Walvis Bay and Sylvia Hill. It is not necessary, however, to enlarge on this here, for the details have been given in an earlier publication (Hart and Marshall, 1951).

Shellfish also have their place in the economic resources of the current, and there is a thriving fishery for the rock lobster (*Jasus lalandii*) on the coast in the southern part of the Benguela region. Although not yet developed, it is possible that squid may some day contribute to a fishery. Frequently large numbers of these animals were seen preying voraciously on saury pikes and lantern fish attracted by the lights of the ship when she was lying at the offshore stations.

Seals

There are several herds of the Cape Fur Seal (*Arctocephalus pusillus*) on the west coast of South Africa. Their breeding-grounds extend from Cape Cross (21° 40′ S.) to Algoa Bay on the south-east coast, and established hauling-out places on the west coast are at Cape Cross, Hollam's Bird Island, several islands near and south of Luderitz Bay, at Kleinsee, Elephant Rock, and some more rocky islets near and south of Saldanha Bay (Rand, 1956). The places where the seals haul out are probably determined largely by the availability of suitable islets, and the topography of the coastline.

These seals are exploited commercially, and during the winter attention is focused on the yearlings of both sexes. During the summer, takings are limited to the bulls in certain rookeries.

Whales

At the beginning of this century some experimental whaling was started in South African waters, and so encouraging were the initial reports that by 1912 some twenty-five companies joined in the quest from the Congo right round to the east coast (Olsen, 1915). Land stations were built, and on the west coast these have operated from time to time at Cape Lopez, Lobito Bay, Elephant Bay, Mossamedes, Port Alexandria, Tiger Bay, Walvis Bay, Luderitz Bay and Saldanha Bay.

Initially this whaling was based on the humpback whale. It appears, however, from the successes of various stations and the failure of others that the original theories concerning the migrations of the humpback up the west coast were open to question. An increasing amount of evidence suggests that the humpbacks, on their northward route from the antarctic, do not arrive at the Cape and progress steadily up the Benguela, but rather that they avoid the cold waters of the current and keep well out to sea, only striking the coast as far north as Portuguese West Africa. Blue whales, fin whales and sei whales are taken at Saldanha Bay, but rarely at the stations north of the Benguela current. Catches of sperm whales at Saldanha Bay have increased in recent years, but it appears that they are mostly found at some distance from the coast.

The small scale of the whaling in the Benguela waters suggests that the current does not form a particularly attractive environment for whales. This of course may be because the whalebone whales in these more northerly latitudes are seeking warmer waters for breeding rather than feeding. It is rather surprising, however, that there appear to be so few sperm whales in the Benguela current. The catches shown in the statistics are poor, and Townsend's charts (1935) also show that very few sperm whales were taken in the Benguela waters. Indeed, these charts showing sperm whales taken to the north of the Benguela, to the west in the south-east trade wind drift and to the south, create the impression that the sperm whale also must specifically avoid the cold coastal waters. These records of the varying intensity of whaling in different areas do not necessarily represent the density of the whale population, and they are coloured by the preference of the whalers for specific types of whale, but nevertheless they are strongly suggestive.

It is more difficult to interpret this avoidance of the Benguela current by the sperm whales than by the whalebone whales. The latter, we know, feed in the Antarctic, but for the former one might expect the rich waters of the Benguela to be an attractive feeding-ground. One can only presume that if the picture created by these records is correct, then there must be some other factor, such as the absence of suitable food organisms, etc., which makes the current unfavourable for the sperm whale.

Guano Islands

The fertile waters of the Benguela current, with their abundant stocks of fish, support enormous populations of sea birds. Practically every rocky promontory and island along the coast is densely inhabited by birds during the nesting-season. The relatively favourable climate with a markedly low rainfall has, in places where the topography has been suitable, led to considerable accretions of guano. Perhaps the most renowned deposits are found on the island of Ichabo (26° 17′ S.) about which an anonymous writer (obscurely described as ex-member of committee, 1845) quotes the following humorous poem:

> There's an island that lies on West Africa's shore,
> Where penguins have lived since the flood or before,
> And raised up a hill there, a mile high or more.
> This hill is all guano, and lately 'tis shown
> That finer potatoes and turnips are grown
> By means of this compost, than ever were known;

And the peach and the nectarine, the apple, the pear,
Attain such a size that the gardeners stare,
And cry, 'Well! I never saw fruit like that 'ere!'
One cabbage thus reared, as a paper maintains
Weighed twenty-one stone, thirteen pounds and six grains,
So no wonder Guano celebrity gains.

Attention was first drawn to the value of the deposits on Ichabo by Morrell (1852)[1], an American sealer. His earlier reports had been rapidly followed up, and by 1845 most of the guano had been removed from Ichabo and ships disappointed in their search there turned to the other islands and coastal deposits. Now, the utilization of the recent deposits is controlled, and for this purpose the islands are divided administratively and geographically into two groups: the 'northern group' comprising the islands to the north of Orange river mouth, and the 'colonial group' extending from 31° S. to the Cape.

Hutchinson (1950), in his monograph on vertebrate excretion, has dealt at some length with the South African deposits, and his work presents us with a very useful summary of what is known of them.

In both groups of islands there are three species of birds which make the major contribution to the deposits. These are as follows:

The Cape Gannet (*Morus capensis* Lichtenstein), (2) the Cape Penguin (*Spheniscus demersus* Linnaeus), and (3) the Trek Duiker (*Phalacrocorax capensis* Sparrman).

In addition to these three species it is probable that the other cormorants make minor contributions. These birds fulfil the principal biological attributes necessary for deposition of guano, in that they are colonial in nesting, and excrete at their nesting-sites. The best guano is formed where there is a minimum of extraneous matter such as sand and feather, etc. introduced into the deposit.

The guano, once deposited, is subjected to weathering, and it is through this process that the characteristic types of guano are developed. Rain and spray both wash the guano, and this results in the leaching of nitrogenous compounds from the deposit, producing the rather inferior *phosphatic* guano, with a low nitrogen content.

There is some evidence that the guano of the 'northern islands', which resembles the modern Peruvian guano, is relatively rich in nitrogen compared with the guano of the 'colonial islands'. The difference may be related to the higher rainfall in the 'colonial group' islands (e.g. Dassen island, see Fig. 3).

It appears that relatively flat islands, which are sufficiently high to allow deposition of guano well clear of the splash zone, form the most favourable substrate for successful accretion. The island of Ichabo in the 'northern group' is the richest producer, and some 2000 tons of guano are deposited there annually. From all of the west South African deposits about 10,000 metric tons are harvested annually, which can be taken as roughly equivalent to the annual deposition. Assuming an average content of phosphate (P_2O_5) of 10%, this would indicate an annual removal of about 440 metric tons of phosphorus from the sea in this region—an amount which would be equivalent to the complete removal of phosphorus from about $5\frac{1}{2}$ km.^{3} of upwelled water. As the total volume of water in the Benguela current is probably of the order of 10^4 km.^{3}, the phosphate removed and deposited as guano must represent a very small part of the available phosphate in the upwelled water.

There is a certain amount of fluctuation in the total annual yield of guano and to some extent this may be related to the availability of food for the birds. In years of catastrophic mortalities of fish (see p. 199) there is some evidence of a fall in guano production, but such variations are by no means so pronounced as on the Peruvian coast. Perhaps this may to some extent be explained by the fact that the region most affected by these catastrophic phenomena is situated to the north of the islands, in

[1] The publication date of his narrative; his voyages took place much earlier.

the vicinity of Walvis Bay, and may only affect the northernmost guano islands. Other adverse phenomena such as abnormal meteorological conditions may have a more general effect over the whole region of the Benguela current.

REVIEW OF THE MAIN FEATURES OF THE BENGUELA CURRENT

The detailed description of the 'William Scoresby's' observations has presented a large number of facts and clearly, before advancing further, we must endeavour to bring these together to create a picture of the current as a whole.

Probably the most obvious feature of this, as of any other upwelling region, is the presence of water at the sea-surface many degrees cooler and incomparably richer in life than that normally found in the open ocean in the same latitude. On account of the temperature anomaly we find, as has been clearly demonstrated by the two 'William Scoresby' surveys, that the surface isotherms are disposed more or less meridionally in contrast to their latitudinal disposition over the greater width of the ocean. This is paralleled in the salinity distribution, and combines with the distribution of many of the other properties investigated in defining the entity of the Benguela current.

Within this general scheme a more detailed picture emerges, and one of the first things to notice is that nearly all of the physical, chemical and biological properties of the current exhibit discontinuity or irregularity both in time and in space. The Benguela current consists of a series of anticyclonic eddies, of interlocking tongues of cool and warmer water, of areas of rich and relatively poor phytoplankton, all of which merge into a complex pattern which is in a constant state of change or flux. This quality of irregularity and instability is in fact one of the features which emphasize the discrete character of this upwelling region.

In the 'William Scoresby's' two surveys there was a great contrast in conditions, and we have presented evidence to show that while in survey II, in spring (September–October), a state of active upwelling was encountered, on survey I, in autumn (March), the current was, at least in part, in a quiescent phase. One cannot be dogmatic about the criterion of normal conditions in such a region, but as the Benguela current is usually looked upon as a region of upwelling, we feel that there is a precedent for accepting conditions of active upwelling as being normal within the current and periods of quiescence as abnormal. It is in this light that we shall proceed to summarize the facts already presented and go on to consider the significance of upwelling in relation to the economy of the ocean as a whole.

Normal conditions

We have remarked on the greater activity of upwelling on the September–October (second) survey of the R.R.S. 'William Scoresby' and perhaps the first and most striking feature can be seen in the chart of surface isotherms (Fig. 7*b*). Here the low surface-temperatures inshore compared with those in the oceanic water to the west, and the configuration of the isotherms, gives one the impression of the cold water masses inshore driving actively out from the coast and thrusting out into the warmer oceanic waters.

This cool, low salinity water (Fig. 8*b*) moving offshore, clearly does not originate uniformly along the coast, but is produced in localized regions. In some cases these may be related to specific features on the sea-bed (Fig. 4), but in general it seems more probable that the dominating effect is that of the local winds in the particular areas. Our results have led us to deduce that while the trade wind far out at sea maintains a tension on the coastal water masses, the local diurnal winds are probably mainly responsible for producing an effective northwards along-shore or offshore drag on the sea-surface and supplying the energy necessary to create these localized centres of upwelling.

In the initial stages of upwelling the lighter surface-water must first be affected and removed away from the coast. To replace it, cooler and denser water must be raised from subsurface depths. This in turn will, however, be transported offshore, and where it meets the lighter surface-waters a relatively strong convection is set up. For example, on the Orange river line of stations the offshore waters are sharply separated from the cooler and denser upwelled waters by a pronounced convection cell (Fig. 37).

Evidently this sharp demarcation is present to a greater or lesser extent along the westward edge of the upwelling waters. The rapid alterations in temperature as this boundary was crossed (Fig. 9) throughout the region bear ample testimony to this, and so it appears that although no geographical boundary is present, the upwelled waters are in fact separated sharply from the warmer oceanic surface-waters lying to the west.

The upwelled waters have a lower temperature and salinity than the offshore surface-waters, and if one compares their T-S relationships with those at the offshore stations, it can be seen that they correspond to those at subsurface depths offshore (Fig. 33*a*) and while they undergo little or no mixing in the process of uplift, they are subjected to some degree of heating when they reach the surface. From this comparison we can determine the depth from which the upwelled water originates and this is seen to be in the layer between 200 and 300 m.

At this depth there is evidence of a subsurface current flowing southwards along the edge of the continental shelf, which we have termed the 'compensation current', and which appears to be the replacement source for water which is upwelled. In this respect it is interesting to note that the compensation current decreases in width in its southward journey (Fig. 34) as would be expected in a replacement flow.

In the waters of the compensation current the content of dissolved oxygen is extremely low and this can be attributed primarily to the source of the water in the oxygen minimum layer which extends over the tropical South Atlantic. Within the compensation current there is a gradual increase in oxygen content from north to south, probably on account of lateral mixing with the adjacent well-oxygenated oceanic waters. The significance of this low oxygen content will be the more evident in the next section of this paper (p. 279).

The waters of the compensation current, and those which are upwelled, have a relatively high content of dissolved inorganic phosphate phosphorus, and the entry of large supplies of this (and probably other) nutrient into the *euphotic* zone is of major importance to the biology of the region.

We have shown that in the coastal waters a large standing crop of phytoplankton was present. The main concentrations were found along the coast in the vicinity of the inshore end of the Sylvia Hill line (25° S.), where the numbers were made up by large quantities of *Chaetoceros* sp. and *Fragillaria karsteni* (at the station closest to the coast). In the warmer more saline oceanic waters, several species of solenoids, *Thallasiothrix longissima*, *Fragillaria karsteni* and *Planktoniella sol* were prominent in the phytoplankton, while in the vicinity of the boundary region the sparse flora contained elements of both the coastal and oceanic floras.

The results of survey II present us, therefore, with a picture of an actively upwelling region, extending in a belt some 80 miles wide along 1000 miles of the western coast of South Africa, an area within which the abundance of flora far exceeds that of the ocean to the west.

Abnormal conditions

On survey I in the autumn (March) we see similar general features, that is, cooler and less saline water along the coast, the eddy-like formation of the surface isotherms (Fig. 7*a*), etc., but in the more detailed features there is a marked contrast with survey II. This is most clearly seen in the vicinity

of Walvis Bay. Here the surface isotherms show a tongue of warm oceanic water pressing towards the coast, and influencing the region as far south as the Sylvia Hill line of stations (25° S.). The water masses on the landward side of this tongue are a mixture (Fig. 33*c*, *d*), evidently derived from oceanic and coastal water types. The penetration of this influence to 25° S. creates in that latitude a reversal of the normal conditions, and there we find the apparent anomaly of warmer and more saline water lying along the coast, with the cooler and less saline water at the offshore stations (WS 986 and 987).

To the north of this wedge an extensive layer of oceanic water extended over the current, typically populated with a flora in which *Planktoniella sol* was a conspicuous member. In the southern part of the wedge, however, the flora was typically that of upwelled water, and inshore on the Sylvia Hill line (25° S.) and Walvis Bay line (23° S.) the largest quantities of chaetocerids encountered on the surveys were found.

It can be seen from Figs. 57 and 65 (pp. 225 and 231) that the highest concentrations of phytoplankton extended over a considerably larger area in survey I than in survey II. This was probably associated with the greater age of the upwelled water, but it may be that the greater stability of the upper water layers also enhanced its growth. In the offshore, unmixed oceanic water, the converse was true, and the phytoplankton there on the average was in fact four or five times less plentiful than on survey II. This may be associated with the more pronounced divergence of subsurface water which occurred seawards of the boundary on the second survey.

This great standing crop of phytoplankton, supporting a correspondingly large crop of zooplankton, must eventually sink down and die, and the nature of the bottom deposits is sufficient evidence that a very large part of the sinking and death takes place in the coastal region. The conditions prevailing at the time of the first survey would certainly have been conducive to this. The meteorological records show that there was little wind, particularly in the vicinity of Walvis Bay, and the currents appear to have been equally sluggish. Indeed, while the ship steamed across these waters, masses of moribund organisms, both phytoplankton and zooplankton, were encountered.

All this organic material sinking to the sea-floor decomposes fairly rapidly, and in so doing will both liberate nutrients and consume oxygen. That nutrients are released in some quantity is strongly suggested by the phosphate sections (Figs. 50–56) which show concentrations of phosphate in the waters of the continental shelf which exceed those in the water upwelling from greater depths. This local nutrient regeneration must play an important part in supplying the dense growth of plants with sufficient nourishment.

The removal of oxygen by decomposition has, however, less beneficial effects. So complete is this process that the water overlying the sea-bed of the continental shelf becomes completely anaerobic, and permits the growth of sulphate-reducing bacteria in the sediment. These bacteria, liberating hydrogen sulphide, enhance the effects of decomposition, and the hydrogen sulphide further reacts with the dissolved oxygen in the overlying waters.

We have already noted that the upwelling water originates from a layer of low dissolved oxygen concentration, and with the further removal of oxygen on the continental shelf it becomes still further depleted. In the normal conditions of flow of the current it does not become seriously reduced, as we can see from the oxygen sections of survey II (Figs. 41–44).

Presumably there is at these times a sufficient flow of water over the region to prevent stagnation. In abnormal conditions, however, the cessation of upwelling, and influx of warmer water on the surface, stopping or even reversing the current, has disastrous effects. These are demonstrated at Walvis Bay, on survey I, where the computed currents (Fig. 34) show a southerly flow in the wedge of oceanic water penetrating into the region, and where the section of dissolved oxygen (Fig. 40) shows that the oxygen depletion actually extended to the sea-surface inshore.

We believe that these events contributed, at least in part, to a small mortality of fish which occurred at Walvis Bay in March 1950. At times such mortalities assume catastrophic proportions (Brongersma-Sanders, 1948) and may seriously affect the fish stocks in this area.

Brongersma-Sanders (1948) has preferred to consider that the mortalities are due to poison originating from the discoloured water which is so frequently coincidental with mortalities. Some of the organisms causing such discolorations are known to be toxic to higher animals. The toxicity, of course, depends on the organism causing the bloom, and in the Walvis Bay region Dr Brongersma-Sanders suggests that a species of *Gymnodinium* may be the origin of such poisons. One of us (T.J.H.) has examined several discolorations or blooms in South African waters, and none of these were caused by that particular genus. *Peridinium triquetrum*, known to have predominated in some of them, has once been recorded in quantity coincidentally with a fish mortality in the Baltic (Lindemann, 1924), but it is a common dominant of polluted inshore waters so that its occurrence near Walvis Bay after a minor mortality might be the result rather than the cause of that phenomenon. This does not, of course, rule out the possibility that Brongersma-Sanders' hypothesis may be proved correct by further work, but from the existing evidence it seems to us more probable that the mortalities are caused by the coincidence of several unfavourable factors, one of which may be toxicity of bloom-forming phytoplankton organisms.

Not much more need be said about the animal populations. The collections of zooplankton have as yet only been analysed from survey I. They show a certain individuality in the general fauna of the current, but, as might be expected, the planktonic animals do not appear to show such a close correlation with the water masses as do the phytoplankton. Apart from this the 'William Scoresby' collections have provided some interesting material in connexion with the wider questions of the distribution of planktonic animals, a subject which lies outside the scope of this paper.

The abundance of the higher animals—the large populations of pelagic fish, seals and birds—and the presence of rich guano islands, are all characteristic features of upwelling regions and bear testimony to their productivity. The apparent scarcity of whales is seemingly anomalous but is perhaps an understandable exception (p. 275).

The discovery of a rich breeding-ground of the pilchard (p. 272) is yet another facet of this interesting region and it emphasizes the fact that many important features may yet be revealed by a more detailed examination of the region.

COMPARISON OF THE BENGUELA CURRENT WITH OTHER UPWELLING REGIONS

The features which we have described in the Benguela current have their parallel in other upwelling regions in the world, and in comparing these one is struck by the surprising similarity of the process and its attendant phenomena, in widely separate geographical localities.

Upwelling is characterized by a divergence of subsurface water masses towards the surface, and as such it is a widespread phenomenon throughout the oceans. By virtue of the effect of the earth's rotation on a current in the ocean the more dense water is found on its left-hand side (looking in the direction of flow) in the northern hemisphere, and on its right-hand side in the southern hemisphere. If the velocity of the current is sufficiently great, more dense (and consequently deeper) water will be lifted to the surface. This may occur along the edge of any suitable current, and may consequently occur either at a solid geographical boundary or at an oceanic boundary with another current. In the latter case we have examples in the divergences in the equatorial regions of the ocean, and in the former the divergences on coastal boundaries of fast-moving currents, for example the Agulhas

current. Such upwelling may vary with the velocity of the current independently of the winds, and we may distinguish it by referring to it as geostrophic upwelling.

On the other hand upwelling may be brought about by the direct influence of winds on the surface-waters, and it is into this category that the major upwelling regions of the world fit. This type of upwelling depends on the lie of the coastline and direction of the winds in relation thereto. It may occur at almost any time throughout the year (e.g. Peru, Benguela, etc.), but in certain regions of seasonal winds it may be a more restricted seasonal phenomenon (e.g. off south-east Arabia or the Indian coasts, Somali coast, Red Sea, etc.). The greater importance of this coastal upwelling derives from the greater depths which it affects. In geostrophic upwelling an upward tilt of isopycnals does occur, and the water brought to lie on the surface depends on the degree of tilt. In coastal upwelling, however, the isopycnals may be thrown up very steeply in response to the action of wind on the sea-surface and deep-lying density layers may be transported right up to the surface. In these conditions waters with a higher nutrient content are brought up to the surface, and the subsequent growth of life makes their presence all the more evident.

There are, as we have said, four *extensive* areas of coastal upwelling, all on the western coasts of the continents of North and South America and Africa, and it is in these that we may look for analogies and differences in the phenomenon.

These currents have certain visible features in common—a negative surface-temperature anomaly, characteristic coastal winds, frequent fogs over the cold water, and arid or desert conditions over the adjacent land. These phenomena, however, may be modified by the topography of the land. Thus, in South and West Africa, there is relatively low-lying land for some 80–100 miles from the sea; here the Namib desert occupies quite a broad strip along the coast, and the sea-breeze can develop a considerable reach over the land. But in Peru the high Cordillera of the Andes is nearer to the coast; it confines the desert to a much narrower strip, and causes the coastal winds to blow more or less parallel to the coast and axis of the Cordillera.

There are also striking differences in the submarine topography of the various regions, which might be expected to influence the process of upwelling. Off South-west Africa the continental shelf is relatively broad compared with that off South America, where the steep slopes of the Andes are projected below the sea-surface to abyssal depths, with only a relatively narrow continental shelf. McEwen (1912) suggested that the upwelling off California showed a striking correlation between the areas of cold water and submerged valleys or other regions where the depth of the sea-bed increased rapidly with distance from the coast. Gunther (1936) could find no evidence of such a correlation off Chile and Peru, and the present work has indicated little or none off South-west Africa. Recently, Yoshida and Mao (1957) have constructed a realistic mathematical model of upwelling off California with little consideration for bottom-effects. There is, therefore, an accumulating amount of evidence which suggests that the actual process of upwelling may not be greatly influenced by the width of the continental shelf in these regions, although there may be effects on the attendant phenomena of the upwelling.

Essentially, the process of upwelling takes the same form in all of these regions. The discrete, eddy-like structure of the surface isotherms is common to all (Peru, Gunther, 1936; California, Sverdrup and Fleming, 1941; Morocco, Currie, unpublished), and the disposition of isopycnals suggests that the basic mechanism is similar in all cases, conforming to the pattern outlined by Sverdrup (1938). We have shown that the same basic mechanism probably occurs in the Benguela current (Fig. 37) and Gunther's density figures for the San Juan line off Peru suggest that a similar vertical circulation is present there also. It is a mechanism, however, which involves rather complex water movements in three dimensions. Fig. 96 may perhaps help to clarify them. It is based on our inferences as to the

water movements in the Benguela current, and is a diagrammatic and somewhat idealized version of them, but we feel that it is a fair representation of the circulation which is probably common to the major upwelling regions (but the mirror image of those in the northern hemisphere).

A striking feature of the Peru current is the very large apparent size of the anti-cyclonic eddies, which far exceed the dimensions of those found in the Benguela and California currents. There is some indication that these large eddies off Peru may conceivably have within them smaller eddies, but in themselves they appear to be peculiar to the Peruvian coast, and one can only assume that it must be constancy in the driving forces which enables them to persist and achieve such large dimensions.

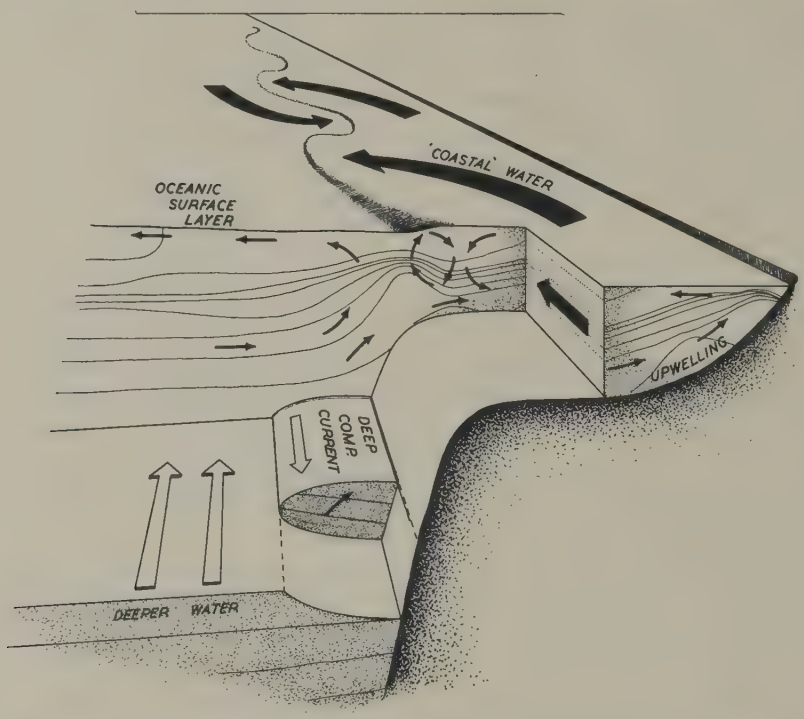

Fig. 96. A perspective diagram showing an idealized picture of the principal horizontal and vertical water-movements in the process of upwelling. The isosteres are represented by the thin lines on the 'cut' faces of the water masses. The shaded sinuous line on the sea-surface represents the continuation of the boundary convection between the upwelled and oceanic surface-waters. The name of the deep compensation current has been abbreviated.

The Peru current itself, of course, is very much more extensive than any of the other upwelling regions, for it runs along the South American coast for nearly 2000 miles. Furthermore it is unique in having within its range the subtropical convergence, and consequently involves subantarctic waters in addition to subtropical waters. By comparison the subtropical convergence in the South Atlantic lies well to the south of South Africa (Deacon, 1933). In spite of its great size, however, the Peru current has a slightly smaller negative temperature anomaly ($-8°$ C.) than the Benguela ($-9°$ C.), and both exceed by far that off California ($-3°$ C.) and Morocco ($-3°$ C.), (Dietrich, 1950).

Upwelling affects similar depths in all of these regions. Gunther (1936) quotes figures of 40–360 m. with a mean at 133 m. in the Peru current. Sverdrup (1941) states that in the California current upwelling was evidently confined to the upper 200 m., and in the Benguela current we have placed it at depths between 200 and 300 m. This removal of water from the 200–300-m. level appears to be accompanied in most cases by a subsurface compensation current. We have described this compensation

current below the Benguela current, flowing southwards and converging with the edge of the continental shelf and bringing water of low oxygen content southwards from the equatorial region. A similar current, better defined, is found off California (Sverdrup and Fleming, 1941) and also below the Peru current, although in the latter case the circulation is more complex. We have mentioned the inclusion of the subtropical convergence in the Peru current. At this convergence, subantarctic water sinks and flows northwards along the coast below the warmer subtropical waters. Off the Peru coast one can identify the southward flowing compensation current, but in 20° S. it meets the northward flowing subantarctic water and is forced under the latter but continues to flow south. A salinity maximum and the low oxygen content are also identifiable to at least 35° S.

The outstanding feature of these compensation currents is their low oxygen content, which in the Benguela current is traceable to the origin of the water in the minimal oxygen layers of the equatorial parts of the oceans. Sverdrup and Fleming (1941) have shown that a further reduction of oxygen takes place with the local decomposition of organic matter. Off the California coast the level of the oxygen minimum lies at a greater depth than off Peru and South-west Africa. Water with an oxygen content of less than 1·0 ml./l. was rarely found at depths of less than 250 m., even at the inshore stations off California, whereas both in the Peru current and Benguela current upwelling brings the low oxygen water up on to the shallower reaches of the continental shelf.

It is clear that there are very close similarities between the abnormal conditions found off South-west Africa, and the 'Callao Painter' and 'Aguaje' off Peru. At the north end of the Peru current periodic incursions of warmer water invade the region where cool upwelled water is usually present. These are referred to as the 'El Nino' current, and Gunther (1936) states that 'one finds in place of the cool Peru Current diverging from the shore, hot poorly saline water of the Equatorial Counter Current flows southwards and converges with it. The rise in temperature kills fish and plankton which then decompose and emit sulphuretted hydrogen on an enormous scale. This is the Callao Painter...'. While the 'Callao Painter' or 'Aguaje'[1] occurs in conjunction with the 'El Nino', it can also be associated with the convergence of warm oceanic water with the coast, and in this respect we find a close parallel with the conditions off Walvis Bay on survey I.

We have expressed the opinion (p. 199) that the low oxygen content of the upwelled water, accentuated under conditions of stagnation or reversed flow of the current, must be a very important factor in the catastrophes off South-west Africa. The coincidence of low oxygen and the manifestations of the Callao Painter is strongly suggestive of a similar sequence of events off the coast of Peru (Burtt, 1852; Currie, 1953*b*).

Perhaps it is significant in this respect that records of pronounced abnormal conditions and fish mortalities are rare on the California coast, where the low oxygen water does not normally appear to be elevated to the proximity of the sea-surface on the continental shelf.

The frequency of records of green diatomaceous mud from the Peru coast (Neaverson, 1934) lend further support to the theory that conditions on the sea-bed of the continental shelf must be virtually anaerobic. Otherwise the chlorophylls and associated pigments would be oxidized to give the sediments a brownish or grey appearance.

Deposition of diatomaceous mud occurs at a much greater depth off Peru than off South-west Africa. Off South-west Africa the diatom mud occurs principally between depths of 50 and 150 m., though it extends to greater depths at the landward end of the Walvis Ridge. The sediments in the deep water beyond the continental shelf are mainly globigerina ooze. Off Peru, however, Neaverson

[1] Evidently some confusion attends the use of the name 'Aguaje'. In the New Velasquez Dictionary it is defined as 'A current in the sea, persistent or periodical; e.g. the Gulf Stream'! Dr Wooster points out to us his impression that 'Aguaje' used in Peru refers to discoloured water of biological origin, only occasionally associated with the 'Callao Painter'.

(*op. cit.*) records diatom mud in abyssal depths; it is usually brown, but sometimes retains a greenish appearance (WS 694, 1216 m.). Tentatively one may ascribe this deposition in deep water to the lesser width of the continental shelf off Peru. The persistence of a green colour of organic origin in these very deep water sediments in the Peru Basin is more difficult to understand, for the sediment must be deposited through water which is fairly well oxygenated.

ORGANIC PRODUCTION IN THE BENGUELA CURRENT

The 'Willlam Scoresby's' surveys were aimed at obtaining a more detailed picture of water-movements and plankton distribution in the Benguela current than had hitherto been available. What we have obtained, therefore, is a more or less instantaneous picture of what was taking place on the two surveys. Such limited observations, particularly in a region of such great variability, can tell us little about such a complex process as organic production. We can, however, say something of the biological activity which was taking place in the particular water masses and from this obtain some idea of how the biological processes within the current compare with those in the adjacent oceanic waters.

On the second survey the greatest quantities of phytoplankton were taken close to the coast between 24° and 26° S., in an area where active upwelling was taking place. Further offshore the quantities decreased, and this suggests that the most favourable conditions for the proliferation of the phytoplankton were present in the very (nutrient) rich, cold water entering the euphotic zone. The upwelling water enriched by the local regneration must have had a very high concentration of dissolved inorganic phosphate-phosphorus, and even this profuse growth of phytoplankton had only reduced it to levels still above 1 mg. at P/m.^{3}. Further seawards, phytoplankton and phosphate both decreased.

In the oceanic surface-water offshore there was a secondary increase in the quantity of phytoplankton, but the amount of phosphate continued to decrease. Qualitatively, however, this offshore phytoplankton was different from that inshore, being dominated by panthalassic or more definitely oceanic species—some of the solenoids in particular for which no doubt the oceanic environment, enriched by lateral mixing from the coastal waters and perhaps also by some divergence seawards of the boundary (see Fig. 96), presented most favourable conditions.

It seems, therefore, that on survey II we have a situation analogous to that described by Sargent and Walker (1948) in the California current. There they found the richest population, dominantly chaetocerids, in the recently upwelled water. From this there was a succession, in the eddies of upwelling water, to a rather sparse warmer water flora in the upwelled water which had been in the surface for the longest time. On survey II in the Benguela current, the eddies were not so far developed, and what we have reported may be a compression of the succession indicated by Sargent and Walker, between the coast and the boundary region, with a separate and distinct oceanic flora to the west of the boundary.

On the first survey, in autumn, the quantity of phytoplankton in the oceanic water was considerably less, by four to five times, than in spring, but there is some evidence that at least in places it may have been richer shortly before the survey was made. At stations WS 996 and 997 the very marked phosphate depletion in the surface-layers, with the presence of a large number of pteropods and numerous faecal pellets, suggests that the low crop of phytoplankton may recently have been much greater and had since been reduced by heavy grazing by the pteropods.

In the coastal waters, however, in the relatively abnormal conditions of the autumn survey (I) the average numbers of phytoplankton were greater than in spring, and the area of high concentration extended farther from the coast. Chaetocerids again dominated in the richest region but not all of the dominant species were the same. Many more *Asterionella japonica*, *Eucampia zoodiacus* and

Stephanopyxis turris were present than in spring. One noteworthy feature is that the richest stations on survey I were found in the coastal waters between 23° and 26° S. where the effects of heating and mixing with more saline water were clearly recognizable. Even amidst this dense flora, relatively great quantities of phosphate were recorded. In this area, as we have noted, many moribund plankton organisms and lines of foam, probably accumulations of dying phytoplankton, were observed on the sea-surface, and the conditions would, therefore, have been conducive to a rapid regeneration of nutrients from the decomposing plankton (Seiwell and Seiwell, 1938). Many resting spores of *Chaetoceros didymum* and *C. subsecundum* occurred in the plankton samples, but we have insufficient data to decide whether these were associated with such conditions or merely exhibit the seasonal change in autumn.

The development of the peak population under such conditions is not altogether surprising, for even with uninhibited exponential growth it must take some time for diatoms to reach such dense concentrations in a newly upwelled water mass, and on this occasion the greater age of the upwelled water and higher temperatures would have favoured such a development.

On both surveys the contrast between the densities of the coastal and oceanic populations of phytoplankton was an outstanding biological feature of the region. It should be specially noted that on survey I the coastal populations reached a figure some *four orders of magnitude* greater than those in the oceanic waters, and on survey II the range was three orders of magnitude. The actual figures are given in Tables 14 and 15 (pp. 224 and 230), and their distribution in Figs. 57 and 65 (pp. 225 and 231).

Even the crude settlement volumes of the net hauls (Tables 14 and 15) suffice to show that the rich inshore phytoplankton of the Benguela current is roughly comparable in quantity to that found in the Peru current (Gunther, 1936) and in the more oceanic waters of the antarctic zone during the main increase (Hart, 1934, 1942). They are significantly poorer than those found in northern antarctic coastal waters (South Georgia) in late spring, but much richer than the values recorded there during the post-maximal decrease and in winter. In the Benguela coastal waters there seems to be but little seasonal falling off in quantity so long as the surface-layers are replenished by upwelling, so that it is quite probable that the total annual production there equals or even exceeds that of the South Georgia area, though the latter (at the height of the spring increase) can amount to 7–10 times the Benguela or Peru averages. These figures from South Georgia in fact furnish by far the greatest standing crop values yet known to us from any part of the world.

The open ocean, we know, presents a relatively stable and uniform environment and this in turn appears to be accompanied by stability in the biological processes occurring in these waters. On the other hand, the dominant physical feature of upwelling regions is their irregularity even under normal conditions and this is paralleled with a constantly changing biological picture.

Unfortunately our knowledge of the upwelling process is still far from being quantitative and until we can measure the processes of advection, eddy diffusion and mixing in the upwelling water we can go no further than to describe a very generalized picture of the environment and conjecture about the processes occurring therein.

Nor do the biological phenomena lend themselves to ease of measurement, continually undergoing rapid and extensive fluctuations. Steeman-Nielsen and Jensen (1957) have shown how the high-standing crop of phytoplankton is accompanied by a high rate of primary production. The transfer of organic matter through the organic cycle is initially dependent on the grazing of the herbivorous animals, and the success of the transfer depends on the efficiency of the grazing process. The high-standing stock of higher animals in the area shows that the extent of the grazing must be very great. Nevertheless plants which are not eaten eventually sink, die and decompose, and in the bottom deposits

of the South-west African region there is evidence that sinking and death of the phytoplankton occurs on a large scale. This, together with the ephemeral nature of the upwelling, leads one to question the efficiency of the grazing and to suppose that it may not reach its potential level, and that much organic matter may be lost at this early stage in the organic cycle.

It is tempting to speculate on the possible interactions of primary production, sinking and grazing in a region such as this, but our data do not permit us to put any time-scale on the processes involved and so at best such a discussion would be truly speculative. Clearly this would be one of the prime considerations in any more extensive a study which might be contemplated in the future. It is quite outside the scope of an exploratory survey such as was made by the 'William Scoresby'.

SUMMARY

The R.R.S. 'William Scoresby' made two surveys of the waters off the South-west African coast as part of a more extensive programme of oceanography and whale-marking in the Atlantic and Indian Oceans.

These surveys, the first in autumn (March) and the second in spring (September–October) 1950, were planned to obtain a more detailed picture of the water movements and biological features of this region than had hitherto been attempted. Furthermore, the comparison of this region with the Peru coastal current which had at an earlier date been surveyed by the same ship and with other upwelling regions was one integral part of the wider field of work, the study of organic production in the oceans.

The report commences with a brief account of the early voyages and previous scientific work in this region, notably referring to the work of the 'Meteor' expedition, 1925–7, some of whose observations were made in South-west African waters.

The oceanographical methods used on these surveys are described together with the various laboratory techniques and methods of analysis which were later used in interpreting the observations. This section on the work of the R.R.S. 'William Scoresby' is concluded with a detailed account of the itinerary of each survey.

A description of the topography of the coastal region of South-west Africa and the adjacent sea-floor follows. An outstanding feature of the coast is an extensive arid desert, the Namib desert, whose existence is intimately connected with the presence of cool surface-waters along the coast. On the sea-floor, the continental shelf has a width of some 40–80 miles and from the edge the bottom slopes away steeply into the abyssal depths of the Cape and Angola basins. These basins are separated by the Walvis Ridge, a prominent feature which connects the continent of Africa to the Central Atlantic ridge.

The wind system over the south-west African region is shown to be divided into two well-defined components, the south-east trade wind which predominates over the oceanic waters and the diurnally variable coastal winds which prevail in a belt extending seawards some 80 miles from the coast. The trade wind can be considered as the eastern limb of the anti-cyclonic circulation of air over the South Atlantic and the coastal winds as a divergence of the coastal boundary of the trade winds, resulting from the extensive diurnal pressure changes over the continent. The coastal wind of importance is S.S.W., which brings warm, moist air from the ocean over the cool coastal waters, and leads to the formation of fogs and the aridity of the land to leeward.

During the surveys, the trade wind was weaker in March (survey I) and better developed in September–October (survey II). The coastal winds were on the whole weak in March and stronger in September–October.

The sea-surface currents are, like the winds, divisible into two clearly defined circulations. In the

region of influence of the trade wind, a N.N.W. flow is induced and this forms the eastern limb of the anti-cyclonic circulation of the South Atlantic. Nearer the coast and sharply demarcated from this drift, the currents are variable, and as the oceanographical observations show, are characterized by pronounced vertical movements. We have restricted the use of the name Benguela current to this coastal circulation in which the upwelling movements occur and have referred to the oceanic circulation as the 'south-east trade wind drift'.

The distribution of temperature and salinity of both surveys has shown that these two currents are characterized by two different types of water—the coastal or upwelled water, and the oceanic water which is warmer and more saline. Varying mixtures of these two types occurred in some areas.

A comparison of the two surveys showed that while in September–October (survey II) active upwelling was taking place over most of the region surveyed, in March (survey I) the waters were more quiescent and a large part of the coastal region was occupied by an influx of mixed oceanic water.

The relationship of the water masses in the south-west African region to those in the South Atlantic as a whole is discussed at some length, and it is evident that the cool, less saline coastal waters are derived from the South Atlantic central water at subsurface depths (200–300 m.) offshore.

A computation of the dynamic height anomalies of the sea-surface relative to the 600 db. surface agrees essentially with the deduced water-movements and emphasizes the eddy-like nature of the coastal circulation. The topography of the 200 db. surface (relative to 600 db.) depends on rather few observations at this depth, but indicates a southerly flow along the edge of and converging with, the continental shelf. It is suggested that this is a replacement flow for the water which is upwelled, and it has been termed the 'compensation current'.

The mechanism of the upwelling has been examined, and it was found to be essentially similar to the process off California described previously by Sverdrup (1938). Where the upwelled waters of the Benguela current meet the warm oceanic waters a convection cell develops, which forms a sharp boundary, and the position of this, although variable, lies some 40–80 miles offshore, in the vicinity of the edge of the continental shelf and the position of divergence in the surface wind system.

The distribution of dissolved oxygen in the subsurface 'compensation current' suggests that the latter is continuous with the oxygen minimum layer in the equatorial parts of the ocean, and may indeed arise from the latter. The impoverishment of oxygen in this water which is evidently the source of the upwelling water, is further accentuated by the decomposition of organic matter on the sea-bed of the continental shelf, and in certain areas anaerobic conditions are created where sulphate-reducing bacteria thrive and liberate hydrogen sulphide into the overlying waters. In March (survey I) the depletion of oxygen extended to the sea-surface inshore at Walvis Bay and we believe this may have contributed to a small mortality of fish which occurred at Walvis Bay during the survey. The association of this phenomenon with the incursion of mixed oceanic water and calm conditions at Walvis Bay suggested a correlation between the fish mortalities and such conditions, and examination of earlier records of winds, strengthens the correlation between mortalities and calms or northerly winds in this area.

The considerable amount of decomposition of organic matter taking place on the sea-bed of the continental shelf led to a further enrichment of the already phosphate-rich upwelled water.

On survey II an attempt was made to determine the total extent of the anaerobic or 'azoic' zone on the sea-floor of the continental shelf. This was found to extend, at least in patches, for a distance of 400 miles along the coast.

The terminology used in the account of the microplankton and the taxonomy of the main groups met with during the two surveys are discussed at length. Part arbitrary groupings, devised solely to aid presentation of these data, are also described in detail. Drastic changes in the accepted practice in

the literature of the subject over the last few years seem to make this essential. For the same reason full notes are given on recent changes in taxonomy of certain individual species better known under earlier names.

The diversity of the microplankton is demonstrated by the full list of all microplankton categories recognized during the routine analyses, and tabulation of the records of frequency of occurrence and of dominance.

The next two subsections deal with the distribution of the main groups of the microplankton, and in particular the distribution of the dominant group, the diatoms; arrayed according to the grouping devised for this purpose. The two surveys are treated separately with the aid of diagrams and tables. This shows that the general pattern of distribution of the more important microplankton species conformed fairly closely to the disposition of the water masses.

In the rich upwelled coastal waters chaetocerids were dominant, with certain markedly neritic species from the other groups (e.g. *Stephanopyxis turris*, *Eucampia zoodiacus*, *Fragilaria karsteni* and *Asterionella japonica*). The extent and average intensity of the rich inshore phytoplankton were greatest during the first (autumn) survey, though the heaviest individual hauls were obtained in spring. Forms such as *Planktoniella sol* and *Thallassiothrix longissima* were typically dominant in the much sparser phytoplankton of the offshore waters, together with certain solenoids during the second survey. The transition zone, which seems nearly to coincide with the hydrologically determined divergence region, usually contained a scanty microplankton consisting mainly of more panthalassic types from either of the main habitats.

The more extensive coastal production in autumn (survey I) with numerous resting spores of the dominant chaetocerids is thought to represent a late stage in the succession of waters earlier enriched by upwelling, since that process was proceeding but weakly at the time. Probably this is not a purely seasonal effect, for upwelling probably persists, intermittently, throughout most of the year. Hence the succession may be repeated several times annually. During the spring survey (II) the rich coastal area was narrower, and the proportions of the dominant species rather different, with few resting spores. Upwelling activity was great, as shown by marked instability of the surface-layers among other hydrological features. Here an early stage in the probable succession is postulated, some of the enriched water having risen to the euphotic zone too recently for the phytoplankton crop to have taken full advantage of it. Attention is drawn to the analogy with conditions observed in the California current by workers benefiting from more complete seasonal coverage (Sargent and Walker 1948).

Conversely, the scanty offshore phytoplankton was much richer during the spring survey than it had been during the autumn. Here it seemed that the increased turbulence occasioned by greater wind stress was proving definitely beneficial to plant production.

In the section on special distributional features, species have been selected whose distribution in the routine hauls seemed best to illustrate either the general distributional trends or divergence from the pattern typical of the group to which they belong. Their distribution is described and charted in detail.

Observations on visibly discoloured sea-water within the area surveyed confirmed that the dark green to opaque black appearance of large areas near Walvis Bay was due to the dense population of inshore diatoms, as Gilchrist (1914) had previously recorded. *Chaetoceros didymum* and *Asterionella japonica* were two of the species mainly responsible. Within this same area more localized brownish discolorations were also seen, and three samples from these showed the development of a definite 'bloom' of *Peridinium triquetrum*, with lesser numbers of *Prorocentrum micans* and diatoms, sometimes associated with lanes of salps and ctenophores dying at the surface. A minor fish-mortality had occurred near Walvis Bay just before. Detailed analyses of these samples are given, and their possible significance in relation to mortality phenomena discussed.

On the second survey one intense red discoloration was seen close inshore in the extreme north of the area, which was found to be due to the ciliate *Cyclotrichium meunieri* Powers (=*Mesodinium rubrum* Lohmann) and its associated symbiotic alga. This is discussed in relation to previous observations of it round Cape Province, and recent revisions of the taxonomy.

A rearrangement of the data concerning the main diatom groups, based on arbitrarily selected distance limits, illustrates the distinction between offshore and inshore diatom floras, and provides some basis for ecological characterization of the species within each of the groups, somewhat on Gran's lines.

This concept is carried a stage further in an attempt at 'ecological characterization' of the more important plankton diatom species of the area. Comparison with their recorded distribution elsewhere shows that they are even more cosmopolitan than was generally recognized hitherto. This lends point to the argument that it is the relative importance of the various forms, rather than their mere presence and absence, that must be studied before the relations between marine plankton floras and their 'conditions of existence' begin to be perceptible. In this there seems to be a basic contrast between the planktonic floras and faunas, for 'presence or absence' is often of real significance in the latter.

The zooplankton has been completely sorted only from survey I. Some groups have been reported on and the findings of these are summarized. The outstanding feature of the zooplankton distribution appeared to be its greater independence of specific water masses than the phytoplankton and a conspicuous patchiness in the distribution of some species.

A brief account is given of other life in the current—notably the fish, seals and whales, and also the guano islands, all of which are outstanding economic features of the region.

Reference is made to a spawning ground of the South African pilchard, located between Walvis Bay and Sylvia Hill. This is a point of some importance but has been dealt with in a separate publication.

Many features of the Benguela current are similar or analogous to those of other upwelling regions and a concluding section is devoted to comparing the main features of the four major upwelling regions of the world. The extraordinary richness of upwelling regions in comparison with the adjacent oceanic waters presents interesting material for speculation on the process of organic production in these environments. At present, however, our knowledge of the magnitude of the processes does not permit any quantitative treatment of this problem.

REFERENCES

AIKAWA, H., 1936. *On the diatom communities in the waters surrounding Japan.* Rec. Oceanogr. Wks. Jap. vol. VIII, no. 1, pp. 1–159, figs. 1–60, tables 1–61.

ALEXANDER, J. E., 1838. *An expedition of discovery into the interior of Africa*, vol. II, 306 pp. London.

ALLEE, W. C. and OESTING, R., 1934. *Winkler's method in the study of the respiration of animals.* Physiol. Zoöl. vol. VII, pp. 509–41.

ALLEN, W. E., 1938. *The Templeton Crocker expedition to the Gulf of California in 1935—the Phytoplankton.* Trans. Amer. Micr. Soc. vol. LVII, no. 4.

ALSTERBERG, G., 1926. *Die Winklerische Bestimmungs methode für in Wasser gelösten elementaren Saurestoff sowie ihre Anwendung bei Anwesenheit oxydierbarer Substanzen.* Biochem. Z. vol. CLXX, p. 30.

ANDERSSON, C. J., 1858. *Reisen in Südwest Afrika bis zum See Ngami in den Jahren 1850–54*, vol. I, 288 pp. Leipzig.

—— 1861. *The Okavango river: a narrative of travel, exploration and adventure*, 364 pp. Hurst and Blackett, London.

—— 1866. *Lake Ngami*, 536 pp. Hurst and Blackett, London.

ANON., 1874. Concerning the wind and upwelling off Kapstadt. *Petermanns geogr. Mitt.* vol. XX, p. 294.

—— 1926. *Massenvernichtung von nutzfischen an der Südwestkuste Afrikas.* Mitt. dtsch. SeefischVer. vol. XLII, pp. 24–5.

—— 1951*a*. *Sea eruptions off S.W. Africa.* Bulawayo Chronicle, N. Rhodesia. 16th Feb., 1951

—— 1951*b*. *Three mud islands appear near Walvis Bay.* Johannesburg Star, S. Africa. 6th Mar., 1951

Anon., 1951*c*. *More sulphur eruptions.* Cape Argus, Cape Town, S. Africa. 8th Mar. 1951

Apstein, C., 1908. *Supplement to Parts* xviii–xxi, *Pflanzendes. Nordischen Planktons.* Nordisches Plankton xxii.

Bachem, Kapt., 1896. *Geographie des Südwestafrikanischen Küste. Kamerum-Kapstadt, Kapstadt-Kamerun.* Ann. Hydrogr. Berl. J. xxiv, pp. 145–8 and 296–300.

Bailey, J. W., 1842. *A sketch of the Infusoria, of the Bacillaria, etc.*, Amer. J. Sci. Arts, vol. xlii, pp. 88–105.

Bailey, L. W., 1862. *Notes on new species of microscopical organisms chiefly from the Para River, South America.* Boston J. Nat. Hist. vol. vii.

Bary, Brian M., 1956. *Notes on ecology, systematics and development of some Mysidacea and Euphausiacea (Crustacea) from New Zealand.* Pacif. Sci. vol. x, pp. 431–67.

Bary, Brian M. and Stuckey, R. G., 1950. *An occurrence in Wellington Harbour of* Cyclotrichium meunieri *Powers, a ciliate causing red water, with some additions to its morphology.* Trans. R. Soc. N.Z. vol. lxxviii, part I, pp. 86–92.

Bobzin, E., 1922. *Vergleichende Betrachung des Klimas und der Kalten Auftriebstromungen an der Südwestafrikanischen und Südarabischen Küste.* Dtsch. übers. met. Beob. Hft. 23, pp. H1–18.

Boden, Brian P., 1950. *Some marine plankton diatoms from the West Coast of South Africa.* Trans. R. Soc. S. Afr. vol. xxxii, part iv.

—— 1955. *Euphausiacea of the Benguela current. First Survey. R.R.S. 'William Scoresby', March 1950.* 'Discovery' Rep. vol. xxvii, pp. 337–76.

Böhnecke, G., 1943. *Auftriebwasser im Atlantischen Ozean.* Ann. Hydrogr. Berl. J. lxxi, pp. 114–17.

Bonde, C. von and Davies, D. H., 1951. *Breeding of pilchards off the west coast of South Africa.* Nature, Lond. vol. clxviii, p. 952.

Boss, G., 1941. *Niederschlagsmengen und salzegehalt des Nebelwassers an der Küste deutsch Südwestafrikas.* Bioklim. Beibl. vol. ii, 8, p. 1.

Bourke, E. G., 1878. *Notes on the meteorology and physical geography of the west coast of Africa, from Cape Verd to the Cape of Good Hope.* Quart. J. R. Met. Soc. vol. iv, p. 25.

Braarud, T., 1945. *A phytoplankton study of the polluted waters of inner Oslo Fjord.* Hvalråd. Skr. no. 28.

Brennecke, W., 1909. *Forschungsreisen der S.M.S. 'Planet' 1906–1907.* Bd. iii. Ozeanographie. s. 133 Berlin.

Bright, K. M. F., 1938. *The South African intertidal zone in relation to ocean currents.* ii and iii. Areas of the west coast. Trans. R. Soc. S. Afr. vol. xxvi, pp. 49–58.

Brongersma-Sanders, M., 1945. *The annual fish mortality near Walvis Bay and its significance for palaeontology.* Arch. néerl. Zool. vol. vii, p. 291.

—— 1947. *On the desirability of research into certain phenomena in the region of upwelling water along the coast of South-west Afrika.* Proc. Acad. Sci. Amst. vol. l, pp. 659–65.

—— 1948. *The importance of upwelling water to vertebrate palaeontology and oil geology.* Verh. Akad. Wet. Amst. 2nd sect. dl. 45, no. 4.

Brown, Robert, 1868. *On the nature of the discoloration of the Arctic seas.* (Read before the Edinburgh Botanical Society in 1867.) J. Bot., Lond.

Buchan, A., 1895. *Report on oceanic circulation based on the observations made on board H.M.S. 'Challenger' and other observations.* Rep. Sci. Res. Voy. 'Challenger'. A summary of the scientific results, part ii, pp. 1–38.

Buchanan, J. Y., 1886. *On the similarities in the physical geography of the great oceans.* Proc. R. Geogr. Soc. Lond. vol. viii, pp. 753–69.

Burtt, J. L., 1852. *On fish destroyed by hydrogen sulphide in the Bay of Callao.* Amer. J. Sci., ser. 2, vol. xiii, pp. 433.

Butlin, K. R., 1949. *Some malodorous activities of sulphate-reducing bacteria.* Proc. Soc. Appl. Bact. vol. xii, pp. 39–42.

Butlin, K. R., Adams, Mary E. and Thomas, Margaret, 1949. *The isolation and cultivation of sulphate-reducing bacteria.* J. Gen. Microbiol. vol. iii, pp. 46–59.

Carillo, D. C. N., 1892. *Estudios sobre las corrientes oceanicas y especialemente de la corriente Humboldt.* Bol. Soc. Geogr. Lima, vol. ii, pp. 72–110.

Classen, Th., 1930. *Periodisches Fischsterben, in Walvis Bay, Südwestafrika.* Palaeobiologica, vol. iii, pp. 1–13.

Cleve, P. T., 1873. *Examination of diatoms found on the surface of the Sea of Java.* K. svenska VetenskAkad. Handl. vol. i, no. 11.

—— 1889. *Pelagiske Diatomeer från Kattegat. Det Videnskabelie Udbytte af Kanonbadden 'Hauchs' Togter i de Danske Have.* pp, 53–6.

—— 1894. *Planktonundersokningar, Cilioflagellater und Diatomaceer.* K. svenska VetenskAkad. Handl. vol. xx, no. 2.

—— 1901. *The seasonal distribution of Atlantic plankton organisms.* Kongl. Vet. och. Vett. Samh. Handl. xvii.

Clowes, A. J., 1950. *An introduction to the hydrology of South African waters.* Fish and Mar. Biol. Surv., Union of S. Africa, Inv. Rep. no. 12.

—— 1954. *Inshore surface currents on the west coast of the Union of South Africa.* Nature, Lond. vol. clxxiii, p. 1003.

Cole, H. A., 1952. *Plankton terminology* (under 'Comments and Communications'). Science, 26 Dec. 1952.

COOPER, L. H. N., 1933. *A system of rational units for reporting nutrient salts in sea water.* J. Cons. int. Explor. Mer, vol. VIII, pp. 331–4.

COPENHAGEN, W. J., 1934. *Occurrence of sulfides in certain areas of the sea-bottom on the South African coast.* Fish. and Mar. Biol. Surv., Union of S. Africa, Rep. no. 11, Inv. Rep. no. 3.

—— 1953. *The periodic mortality of fish in the Walvis Region. A phenomenon within the Benguela Current.* Dept. of Comm. and Indust., Union of S. Africa. Division of Fisheries Inv. Rep., no. 14.

CROWE, P. R., 1951. *The trade wind circulation of the world.* Trans. Inst. Brit. Geogr., no. 15, pp. 37–56.

—— 1952. *The seasonal variation in the strength of the trades.* Trans. Inst. Brit. Geogr., no. 16.

CUPP, E. E., 1943. *Marine plankton diatoms of the west coast of North America.* Bull. Scripps Instn. Oceanogr. Non-tech. vol. V, no. 1, pp. 1–238, figs. 1–168, pls. 1–5.

CURRIE, R. I., 1952. *The Benguela current.* Assoc. Océanogr. Phys. Procès-Verbaux, vol. V, 155.

—— 1953*a*. *Upwelling in the Benguela current.* Nature, Lond. vol. CLXXI, p. 497.

—— 1953*b*. *The Callao painter.* Weather, vol. III, no. 10, pp. 308–11.

DANKLEMAN, A. VON, 1878. *Die Meteorologischen Beobachtungen der Gussfeldt'schen Loango Expedition.* Leipzig.

DARWIN, CHARLES, 1839. *Journal of Researches into the Natural History and Geology of the Countries visited during the voyage of H.M.S. Beagle round the world, under the command of Capt. Fitzroy, R.N.* John Murray, London.

DAWSON, E. Y., 1950. *A note on the vegetation of a new coastal upwelling area off Baja, California.* J. Mar. Res. vol. IX, p. 65.

—— 1951. *A further study of upwelling and associated vegetation along Pacific Baja, California, Mexico.* J. Mar. Res. vol. X, pp. 39–58.

DEACON, G. E. R., 1933. *A general account of the hydrology of the South Atlantic Ocean.* Discovery Rep. vol. VII, pp. 171–238.

—— 1937. *The hydrology of the Southern Ocean.* Discovery Rep. vol. XV, pp. 1–124.

DEFANT, A., 1936. *Das Kaltwasserauftriebsgebiet vor der Küste Südwestafrikas.* Landerkdl. Forsch., Festchr. N. Krebs., pp. 52–66.

—— 1951. *Windstau und Auftrieb an ozeanischen Küsten.* Arch. Met., Wien, Serie A, Bd. IV, pp. 296–308.

—— 1952. *Theoretische Überlegungen zum Phänomen des Windstaus und des Auftriebes an ozeanischen Küste.* Dtsch. hydrogr. Z. Bd. V, pp. 69–80.

DIETRICH, G., 1935*a*. *Aufbau und Dynamik des südlichen Agulhas stromgebietes.* Veröff. Inst. Meeresk. Univ. Berl. Ser. A, Hft. 27, 79 pp.

—— 1935*b*. *Zur Dynamik des Atlantischen Zweiges des Agulhasströmes.* Ann. Hydrogr. Berl. J. LXIII, pp. 383–7.

—— 1936. *Aufbau und Bewegung von Golfstrom und Agulhasstrom, eine vergleichende Betrachtung.* Naturwissenschaften, vol. XXIV, pp. 225–30.

—— 1950. *Kontinental Einflusse auf T und S des Ozeanwassers.* Dtsch. hydrogr. Z. Bd. III, p. 33.

DINKLAGE, KAPT. L., 1875. *Aus Briefen deutscher Kapitaine Callao, Jan–Feb., 1874.* Hansa, 1875, pp. 56 ff.

DOVE, K., 1894. *Beiträge zur Geographie von Südwestafrika.* Petermanns geogr. Mitt. vol. XL, pp. 60–4, 100–6, and 172–5.

—— 1898. *Deutsch Südwestafrika.* Petermanns geogr. Mitt. Erganzungsbd. 26, pt. 120, 93 pp.

DUROV, S. A. and TURZHOVA, M. P., 1947. *Determination of the total content of hydrogen sulphide and dissolved oxygen in waters.* Gidrokhim. Mat. vol. XIII, pp. 109–19.

EDEN, T. E., Jnr., 1846. *The search for nitre and the true nature of guano, being an account of a voyage to south-west Africa, and also a description of minerals found there and of the guano islands in that part of the world.* R. Groombridge and Sons, Paternoster Row.

EHRENBERG, C. G., 1838. *Die Infusionsthierchen als vollkommene Organismen.* Leopold Voss, Leipzig.

—— 1843. *Verbreitung und Einfluss des Mikroskopischen Lebens in Sud- und Nord-Amerika.* Abh. dtsch. Akad. Wiss. Berl. 1841, pp. 291–446.

—— 1854. *Mikrogeologie. Das Erden und Felsen schaffende wirken des unsichtbar Kleinen selbständigen Lebens auf der Erde.* Leipzig.

EKMAN, SVEN, 1935. *Tiergeographie des Meeres.* Leipzig Akad. Verlagsges.

—— 1953. *Zoogeography of the sea.* Sidgwick and Jackson Ltd, London.

EKMAN, V. W., 1905. *On the influence of the earth's rotation on ocean currents.* Ark. Math. Astr. Fys. Bd. II, no. 11.

ENGELER, E., 1910. *Periodische und unperiodische Schwankungen der Benguela Strömung.* Ann. Hydrogr. Berl. J. XXXVIII, pp. 475, 536 and 601.

EX-MEMBER OF THE COMMITTEE, 1845. *The African guano trade.* Naut. Mag., Enlarged Ser., no. 11, pp. 619–66.

FINDLAY, A. G., 1867. *A sailing directory for the Ethiopic or South Atlantic Ocean, including the coasts of South America and Africa,* 5th ed. 691 pp. Richard Holmes Laurie, London.

FRANZ, A., 1920. *Beiträge zur Ozeanographie und Klimatologie der Deutsch Süd-Westafrikanischen Küste nach Beobachtungen von S.M.S. 'Möwe'.* Arch. dtsch. Seewarte, vol. XXXVIII, no. 1; also Ann. Hydrogr. Berl. J. XLIX, 1921, pp. 139–40.

FRITSCH, F. E., 1935. *The structure and reproduction of the algae,* part I, Univ. Press, Cambridge.

FRITSCH, F. E., 1945. *The structure and reproduction of the algae*, 2nd ed. Univ. Press, Cambridge.

GAARDER, KAREN RINGDAL, 1951. *Bacillariophyceae from the 'Michael Sars' North Atlantic Deep Sea Expedition 1910.* Rep. Sars N. Atl. Deep Sea Exped. vol. II, no. 2.

GALTON, F., 1889. *Narrative of an explorer in South Africa, 1851. Damaraland.* Ward Lock and Co., London.

GILCHRIST, J. D. F., 1903. *Currents on the South African coast as indicated by the course of drift bottles.* Marine Invest. in South Africa, vol. II.

—— 1914. *An enquiry into fluctuations in fish supply on the South African Coast.* Mar. biol. Rep., Cape T. Rep. 2 for year ending 30 June 1914. Art. 2, pp. 8–35.

GOLOLOBOV, YA. K., 1953. *The thickness of the oxygen–hydrogen sulphide layer in the Black Sea.* Gidrokhim. Mat. vol. XXI, pp. 3–9.

GRAN, H. H., 1902. *Das Plankton des Norvegischen Nordmeeres von biologischen und hydrographischen Gesichtpunkten behandelt.* Rep. Norweg. Fish. Invest. vol. II, no. 5.

—— 1905. *Diatomeen* in Brandt, *Nordisches Plankton.* Botanischer Teil, 1903–8, pp. 1–146 Kiel u. Leipzig.

—— 1912. *Pelagic plant life* in Murray and Hjort *Depths of the Ocean.* Macmillan and Co., London.

—— 1932. *Phytoplankton, methods and problems.* J. Cons. Int. Explor. Mer. vol. VII, pp. 343–58.

GRAN, H. H. and BRAARUD, TRYGVE, 1935. *A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry and turbidity).* J. Biol. Bd. Can. vol. I, no. 5.

GRAN, H. H. and YENDO, K., 1914. *Japanese Diatoms: I. On Chaetoceros. II. On Stephanopyxis.* Vid. Skrift. i Nat. Natur. Klasse, 1913, no. 8.

GROEN, PIER, 1948. *Methods for estimating dynamic slopes and currents in shallow water.* J. Mar. Res. vol. VII, p. 313.

GRUNOW, A., 1863. *Ueber einige neue und ungenügend bekannte Arten und Gattungen von Diatomaceen.* Verh. zool.-bot. Ges. Wien, vol. XII.

GRUNOW, A.. ex VAN HEURCK, H., 1881. *Synopsis des Diatomées de Belgique.* Anvers.

GUNTHER, E. R., 1936*a*. *A report on oceanographical investigations in the Peru coastal current.* Discovery Rep. vol. XIII, pp. 109–276.

—— 1936*b*. *Variations in the behaviour of the Peru coastal current, with an historical introduction.* Geogr. J. vol. LXXXVIII, pp. 37–65.

HALL, F. G., 1929. *Oxygen consumption in marine fishes.* Amer. J. Physiol. vol. LXXXVIII, p. 212.

HANSEN, W., 1951. *Beobachtung des Windstaus und Triftstroms im Modellkanal.* Dtsch. hydrogr. Z. Bd. IV, p. 81.

HARDY, A. C., 1923. *Notes on the Atlantic plankton taken off the East Coast of England in 1921 and 1922.* Publ. Circ. Cons. Explor. Mer, no. 78.

HART, T. J., 1934*a*. *On the phytoplankton of the South-west Atlantic and the Bellingshausen Sea, 1929–31.* Discovery Rep. vol. VIII, pp. 1–268.

—— 1934*b*. *Red 'water-bloom' in South African seas.* Nature, Lond. vol. CXXXIV, pp. 459–60.

—— 1942. *Phytoplankton periodicity in Antarctic surface waters.* Discovery Rep. vol. XXI, pp. 261–356.

—— 1943. *Darwin and water-bloom.* Nature, Lond. vol. CLVI, p. 661.

—— 1953. *Plankton of the Benguela current.* Nature, Lond. vol. CLXXI, p. 631.

HART, T. J. and MARSHALL, N. B., 1951. *Breeding grounds of pilchards off the coast of South-west Africa.* Nature, Lond. vol. CLXVIII, p. 272.

HARVEY, H. W., 1934. *Measurement of phytoplankton population.* J. Mar. Biol. Ass. U.K. vol. XIX, pp. 761–74.

HELLAND-HANSEN, B., 1918. *Nogen hydrografiske metoder.* Forh. skand. naturf. Møte, vol. XVI, pp. 357–9.

HENDERSON, I. F. and HENDERSON, W. D., revised KENNETH, JOHN H., 1953. *Hendersons' dictionary of scientific terms*, 5th ed. Oliver and Boyd, Edinburgh and London.

HENDEY, N. I., 1937. *The planktonic diatoms of southern seas.* Discovery Rep. vol. XVI, pp. 151–364, pls. VI–XIII.

—— 1951. *Littoral diatoms of Chichester Harbour with special reference to fouling.* J. R. Micr. Soc. vol. LXXI, pp. 1–86.

HENTSCHEL, E., 1928. *Die Grundzüge der Planktonverteilung im Südatlantischen ozeans.* Int. Rev. Hydrobiol. vol. XXI, pp. 1–16.

—— 1936. *Allgemeine Biologie des Südatlantischen Ozeans.* Wiss. Ergebn. dtsch. atlant. Exped. 'Meteor', vol. XI.

HENTSCHEL, E. and WATTENBERG, H., 1930. *Plankton und Phosphat in der Oberflächenschicht des Südatlantischen Ozeans.* Ann. Hydrogr. Berl. J. LVIII, pp. 273–7.

HESSNER, —, 1892. *Hydrographische Bemerkungen von der Westküste Südafrikas.* Ann. Hydrogr. Berl. J. XX, pp. 256–7.

HIDAKA, KOJI, 1953. *A contribution to the theory of upwelling.* A. and M. College of Texas, Project 24.

HIDAKA, K. and AKIBA, Y., 1955. *Upwelling induced by a circular wind system.* Rec. Oceanogr. Wks. Jap. vol. II, pp. 7–18.

HIKOSAKA, SHIGEO, 1955. *On the vertical distributions of density and upwellings in a cold water mass.* Rec. Oceanogr. Wks. Jap. vol. II, no. 1.

HOAR, W. S., BLACK, V. S. and BLACK, E. C., 1951. *Some aspects of the physiology of fish.* III. E. C. Black: *Respiration in fishes.* Univ. of Toronto Biol. Ser. no. 59.

HÖLLER, E., 1935. *Klimatographische Witterungschilderung Südwestafrikanischens Gebiet des Atlantischen.* Ann. Hydrogr. Berl. J. LXIII, pp. 320–1.

HUSTEDT, F., 1927–37. *Die Kieselalgen...* in Rabenhorst's *Kryptogamenflora.* 1927–30, part I, 1–5 Teil, part II, 1–5 Teil (1931–7), Leipzig.

HUTCHINSON, G. E., 1938. *Oxygen deficit and the productivity and typology of lakes.* Int. Rev. Hydrobiol. vol. XXXVI, p. 336.

—— 1950. *Survey of contemporary knowledge of biogeochemistry. 3, Biogeochemistry of vertebrate excretion.* Bull. Amer. Mus. Nat. Hist. vol. XCVI, pp. 554.

HYDROGRAPHIC DEPARTMENT, 1939. *Africa Pilot,* Part II. *Rio del Rey to Cape Hangklip.* 9th ed. Stationery Office, London.

HYDROGRAPHIC OFFICE, 1945. *Quarterly surface current charts of the Atlantic Ocean.* Publication M.O. 466, Stationery Office, London.

ILES, E. J., 1953. *A preliminary report on the Ostracoda of the Benguela current.* Discovery Rep. vol. XXVI, pp. 259–80.

ISAAC, W. E., 1937. *South African coastal waters in relation to ocean currents.* Geogr. Rev. vol. XXVII, pp. 651–64.

JACKSON, S. P., 1951. *The climates of South Africa.* S. Afr. Geogr. J. vol. XXXIII, pp. 1–21.

JANKE, J., 1920. *Strömungen im Golf von Guinea.* Arch. dtsch. Seewarte, vol. XXXVIII, p. 16.

JEFFRYS, A., 1923. *The effect of a steady wind on the sea level near a straight shore.* Phil. Mag. vol. XLVI, pp. 115–25.

JOHN, D. D., 1936. *The southern species of the genus* Euphausia. Discovery Rep. vol. XIV, pp. 193–324.

JOHNSTONE, J. J., 1908. *Conditions of life in the sea.* Cambridge Biological Series. Univ. Press, Cambridge, England.

JOHNSTONE, J. J., SCOTT, A. and CHADWICK, H. C., 1924. *The Marine Plankton.* Univ. Press, Liverpool.

JONES, N. S., 1955. *Cumacea of the Benguela current.* Discovery Rep. vol. XXVII, pp. 279–92.

K——, E., 1907. *Die Wind und Stromveshältnisse vor der Westküste von Afrika.* Ann. Hydrogr. Berl. J. XXXV, p. 482.

KARSTEN, G., 1906. *Das Phytoplankton des Atlantischen Ozeans nach dem material der deutschen Tiefsee-Expedition 1898–1899.* Wiss. Ergebn. 'Valdivia' Bd. II, 2nd Teil.

KEMP, S., HARDY, A. C. and MACKINTOSH, N. A., 1929. *The Discovery Investigations. Objects, Equipment and Methods.* Discovery Rep. vol. I, pp. 141–232.

KOCH, —, 1888. *Beobachtungen an der Westküste von Benguela und Mossamedes.* Ann. Hydrogr. Berl. J. XVI, pp. 19–21.

KOFOID, C. A., 1919. *The morphological interpretation of the structure of* Noctiluca, *and its bearings on the status of the* Cystoflagellata (*Haeckel*). Univ. Calif. Publ. Zool. vol. XIX, pp. 317–34.

KOFOID, C. A. and CAMPBELL, A. S., 1929. *A conspectus of the marine and freshwater Ciliata belonging to the suborder Tintinnoinea, with descriptions of new species principally from the Agassiz Expedition to the Eastern Tropical Pacific, 1904–5.* Univ. Calif. Publ. Zool. vol. XXXIV, pp. 404.

KOLBE, R. W., 1957. *Sediment cores from the Indian Ocean. Fasc. I. Diatoms from equatorial Indian Ocean cores.* Rep. Swed. Deep-Sea Exped. 1947–8, vol. IX, pp. 1–50.

KOPPEN, W., 1932. *Feuchtluftwasten Aufquellwasser und Lebensmenge.* Ann. Hydrogr. Berl. J. LX, pp. 468–9.

KREY, J., 1939. *Die Bestimmung des Chlorophylls in Meerwasser-Schöpfproben.* J. Cons. vol. XIV, pp. 201–9.

KUTZING, F. T., 1844. *Die Kieselschaligen Bacillarien oder Diatomeen.* Nordhausen.

LAVALLE Y GARCIA, J. A., 1917. *La contra corriente ecuatorial como causa determinante de fenoneno marino conocido con el nombre de 'Aguaje'.* Bol. Soc. Geogr. Lima, vol. XXXIII, pp. 313–30.

LEBOUR, M. V., 1925. *The dinoflagellates of Northern Seas.* Mar. Biol. Ass. U.K., Plymouth.

—— 1930. *The planktonic diatoms of northern seas.* Ray Society, London.

—— 1954. *The planktonic decapod crustacea and stomatopoda of the Benguela current. Part I. First Survey, R.R.S. 'William Scoresby' March 1950.* Discovery Rep. vol. XXVII, pp. 219–34.

LINDEMANN, E., 1924. *Der Bau der Hülle bei* Heterocapsa *und* Kryptoperidinium foliaceum (*Stein*). Bot. Arch. vol. V, pp. 114–20.

LLOYD, BLODWEN, 1926. *Character and conditions of life of marine phytoplankton.* J. Ecol. vol. XIV, pp. 92–110.

LOHMANN, H., 1908. *Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres am Plankton.* Wiss. Meeresuntersuch. Bd. X.

LONGARD, J. R. and BANKS, R. E., 1952. *Wind induced vertical movement of the water on an open coast.* Trans. Amer. geophys. Un. vol. XXXIII (3), pp. 377–80.

LUCAS, C. E., 1947. *The ecological effects of external metabolites.* Biol. Rev. vol. XXII, pp. 270–95.

LUDERITZ, F. A. E., 1884. *Bemerkungen über Sandwich Harbour und Walfisch Bay.* Ann. Hydrogr. Berl. J. XII, p. 651.

LUMBY, J. R., 1955. *Depth of the wind produced homogeneous layer in the ocean.* Ministry of Agric., Fish. and Food, Fishery Investigations, Series II, 20, no. 2, 12 pp.

MACARTNEY, J., 1810. *Observations upon luminous animals.* Phil. Trans. vol. C, pp. 258–93.

MCEWEN, G. F., 1912. *The distribution of ocean temperatures along the west coast of North America deduced from Ekman's theory of upwelling of cold water from the adjacent ocean depths.* Int. Rev. Hydrobiol. vol. V, pp. 243–86.

—— 1934. *Rate of upwelling in the region of San Diego computed from serial temperatures.* Proc. 5th Pacif. Sci. Congr. 1933, vol. III, p. 1763.

McEwen, G. F., 1948. *The dynamics of large horizontal eddies (axes vertical) in the ocean off southern California.* J. Mar. Res. vol. VII, p. 188.

Major, R. H., 1877. *The discoveries of Prince Henry the navigator, and their results*, 2nd ed. London.

Mangin, L., 1908. *Observations sur les Diatomées.* Ann. Sci. nat. (a) 9e sér. vol. VIII, Paris.

—— 1912. *Phytoplancton de la croisière du René dans l'Atlantique.* Ann. Inst. océanogr., Paris. vol. IV.

Marchand, J. M., 1928. *The nature of sea-floor deposits in certain regions of the west coast.* Special Rep. no. 5, Fish and Mar. Biol. Surv., Union of S. Africa, Rep. no. 6.

Marmer, H. A., 1951. *The Peru and Nino currents.* Geogr. Rev. vol. XLI, pp. 337–8.

Marshall, S. M., 1933. *The production of microplankton in the Great Barrier Reef Region.* Great Barrier Reef Expedition, 1928–9. Sci. Rep. Gr. Barrier Reef Exped. vol. II, no. 5, pp. 111–57.

Martineau, D. P., 1953. *The influence of the current systems and lateral mixing on Antarctic Intermediate water in the South Atlantic.* Woods Hole. Unpubl. Manuscript. 53/72.

Marumo, R., 1953. *On the diatom plankton of the Antarctic Ocean in summer from 1946–1952.* Rec. Oceanogr. Wks Jap. vol. I, no. 2.

—— 1954. *Diatom plankton in the South of Cape Shionomisaki in 1953.* Oceanogr. Mag. vol. VI, no. 3.

Mayo, The Earl of, 1883. *A journey from Mossamedes to the River Cunéné, South West Africa.* Discussion by Mr Francis Galton. Proc. Roy. Geogr. Soc. vol. V, pp. 458–73.

Mears, E. G., 1944*a*. *The Ocean Current called 'The Child'.* Rep. Smithson. Instn, 1943, pp. 245–51.

—— 1944*b*. *Counterpart of the Davidson current.* Nature, Lond. vol. CLIII, pp. 346–7.

Merz, A., 1925. *Karten der Oberflächenströmungen südlich Afrikas in Jan. Mai. Juli. Okt.* Unpublished, Institut für Meeresk., Berlin.

Meunier, A., 1913. *Microplankton de la Mer Flamande I^re^ Partie: Le genre Chaetoceros Ehrg.* Mém. Mus. Hist. nat. Belg., 3, Brussels.

Meyer, H. H. F., 1923. *Die Oberflächenströmungen des Atlantischen Ozeans im Februar.* Veröff. Inst. Meeresk. Univ. Berl. A, Hft. XI, pp. 1–35.

Michael, Ellis L., 1921. *Effect of upwelling water upon the organic fertility of the sea in the region of Southern California.* Proc. 1st. Pacif. Sci. Congr., 1921, pp. 555–95.

Miller, A. R., 1950. *A study of mixing processes over the edge of the continental shelf.* J. Mar. Res. vol. IX, p. 145.

Moberg, E. G., 1928. *The interrelation between diatoms, their chemical environment and upwelling water in the sea, off the coast of Southern California.* Proc. Nat. Acad. Sci., Wash., vol. XIV, pp. 511–18.

Montgomery, R. B., 1938. *Circulation in upper layers of the southern North Atlantic deduced with the use of isentropic analysis.* Pap. phys. Oceanogr. vol. VI, no. 2.

Monts, von, 1877. *Wasser-temperatur im Agulhas Ström und der süd küste Afrika.* Ann. Hydrogr. Berl. J. V, pp. 352–3.

Morrell, B., 1852. *Morrell's narrative of a voyage to the south and west coasts of Afrika: containing the information from which the present trade in guano from certain islands on this coast originated*, 144 pp. Whittaker and Co., London.

Morton, J. E., 1954. *The pelagic Mollusca of the Benguela Current, Part I. First survey, R.R.S. 'William Scoresby', March 1950.* Discovery Rep. vol. XXVII, pp. 163–200.

Muffling, Kapt. F. von, 1911. *Wind, Witterung und Seeverhältnisse an der Küste südwestafrikas, Jan.-Mar., 1910.* Ann. Hydrogr. Berl. J. XXXIX, p. 47.

Mühry, A., 1864. *Die Meeresströmungen an der Südspitze Afrikas.* Petermanns geogr. Mitt. vol. X, pp. 34–5.

Muir, J., 1932. *The beach drift of South Africa.* J. Bot. Soc. S. Afr. pt. 18, p. 5.

Murray, J., 1888. *On the effects of winds on the distribution of temperature in the sea and fresh water lochs of the west of Scotland.* Scot. Geogr. Mag. vol. IV, p. 345.

—— 1891. *On the temperature of the salt and fresh water lochs of the west of Scotland at different depths and seasons during the years 1887 and 1888.* Proc. R. Soc. Edinb. vol. XVIII, p. 139.

Neaverson, E., 1934. *The sea-floor deposits. I. General characters and distribution.* Discovery Rep. vol. IX, pp. 295–350.

Okamura, K., 1907. *Some* Chaetoceras *and* Peragallia *of Japan.* Bot. Mag., Tokyo, vol. XXI.

Olsen, Ørjan, 1914–15. *Hvaler og Hvalfangst i Sydafrika.* Bergens Mus. Aarb. no. 5, pp. 1–56.

Owen, W. F. W., 1833. *Narrative of voyages to explore the shores of Africa, Arabia and Madagascar*, vol. I, 260 pp. J. and J. Harper, New York.

Parr, A. E., 1938*a*. *Isopycnic analysis of current flow by means of identifying properties.* J. Mar. Res. vol. I, pp. 133–54.

—— 1938*b*. *On the validity of the dynamic topographic method for the determination of ocean current trajectories.* J. Mar. Res. vol. I, pp. 119–32.

—— 1938*c*. *Analysis of current profiles by a study of pycnomeric distortion and identifying properties.* J. Mar. Res. vol. I, pp. 269–90.

Paulsen, Ove, 1909. *Plankton Investigations in the waters round Iceland and in the North Atlantic, 1904.* Medd. Komm. Havundersøg., Kbh., Ser. Plankton I, no. 8.

PAVILLARD, J., 1911. *Observations sur les Diatomées.* Bull. Soc. Bot. Fr. vol. LVIII, pp. 21–9.

—— 1921. *Sur la Reproduction du* Chaetoceros Eibenii *Meunier.* C.R. Acad. Sci., Paris, vol. CLXXII.

PECHUËL-LOESCHE, E., 1882. *Die Loango Expedition.* Abt. 3, pp. 16 *et seq.* Leipzig.

PERAGALLO, H., 1892. *Monographie du genre* Rhizosolenia *et des quelques genres-voisins.* La Diatomiste I, pp. 79–82, 92–117.

PEZET, F. A., 1896. *La Contra-corriente 'El Nino'.* Bol. Soc. Geogr. Lima, vol. V, pp. 457–61.

POHLENZ, KAPT., 1908. *Reise von Swakop nach Durban.* Ann. Hydrogr. Berl. J. XXXVI, pp. 225–8.

POLLAK, M. J., 1950. *Notes on determining the depth of sampling in serial oceanographic observations.* J. Mar. Res. vol. IX, pp. 17–20.

POWERS, P. B. A., 1932. Cyclotrichium meunieri *sp.nov.* (*Protozoa, Ciliata*)*: cause of Red Water in the Gulf of Maine.* Biol. Bull., Woods' Hole, vol. LXIII, no. 1, pp. 74–80.

PRUTHI, H. S., 1927. *Preliminary observations on the relative importance of the various factors responsible for the death of fishes in polluted waters.* J. Mar. Biol. Ass. U.K. vol. XIV, p. 729.

RALFS, J., 1861. *Diatoms,* in Pritchard, A., *History of the infusoria,* 4th ed.

RAND, R. W., 1956. *The Cape Fur Seal,* Arctocephalus pusillus (*Schreber*). *Its general characteristics and moult.* Dept. of Comm. and Indust., Union of S. Africa, Division of Fisheries, Inv. Rep. no. 21.

RAVENSTEIN, E. G., 1898. *A journal of the first voyage of Vasco da Gama, 1497–9,* vol. XCIX, Hakluyt Society, London.

—— 1900. *The voyages of Diogo Cão and Bartholomeu Dias, 1482–1488.* Geogr. J. vol. XVI, pp. 625–55.

REINKE, KAPT., 1896. *Kapstadt—Loanda.* Ann. Hydrogr. Berl. J. XXIV, pp. 529–34.

RENNELL, J., 1832. *An investigation of the currents of the Atlantic Ocean and of those which prevail between the Indian Ocean and the Atlantic,* 359 pp. Rivington, London.

REUNING, E., 1925. *Gediegen Schwefel in der Küstenzone Südwestafrikas.* Zbl. Miner. Geol. Paläont. Sect. A, pp. 86–94.

RICHARDS, F. A. with THOMPSON, T. G., 1952. *The estimation and characterisation of plankton populations by pigment analyses.* II. *A spectrophotometric method for the estimation of plankton pigments.* J. Mar. Res. vol. XI, pp. 156–72.

RILEY, G. A., 1938. *The measurement of phytoplankton.* Inter. Rev. Hydrobiol. vol. XXXVI, pp. 371–3.

—— 1951. *Oxygen, phosphate and nitrate in the Atlantic Ocean.* Bull. Bingham Oceanogr. Coll. vol. XIII, Art. 1.

ROSS, Captain Sir JAMES CLARK, 1847. *Voyage of discovery and research in the southern and antarctic regions during the years 1839–43,* 2 vols. John Murray, London.

ROSSBY, C.-G. and MONTGOMERY, R. B., 1935. *The layer of frictional influence in wind and ocean currents.* Pap. Phys. Oceanogr. vol. III, no. 3, pp. 1–101.

ROYAL NAVAL METEOROLOGICAL SERVICE AND SOUTH AFRICAN AIR FORCE, 1944. *Weather on the coasts of Southern Africa,* vol. II, pts 1 and 2. Cape Times Ltd, Union of S. Africa.

SAINT-GUILY, B., 1956. *Sur la Théorie des Courants Marins induits par le vent.* Ann. Inst. Océanogr. Paris, vol. XXXIII, 1, 64 pp.

SAITO, Y., 1956. *The theory of the transient state concerning upwelling and coastal current.* Trans. Amer. Geophys. Un. vol. XXXVII, 1, pp. 38–42.

SANDSTROM, W. J., 1919. *The hydrodynamics of the Canadian Atlantic waters.* Canadian Fish Exped. 1914–15, pp. 221–403.

SARGENT, MARSTON C. and WALKER, THEODORE J., 1948. *Diatom populations associated with eddies off Southern California in 1941.* J. Mar. Res. vol. VII, no. 3, pp. 490–505.

SCHENK, A., 1901. *Ueber Eine im vorigen Jahre in der Walfisch baai neu entstandene und wieder verschurumdene Insel, über welche wir. F. W. Waldron nähere Nachrichten verdanken.* Z. dtsch. geol. Ges. vol. LIII, pp. 55–6.

SCHERHAG, R., 1937. *Die Abkuhlung von warmluft über kalteren meeresgebieten.* Ann. Hydrogr. Berl. J. LXV, p. 581.

SCHILLER, J., 1933–37. *Dinoflagellatae,* in Rabenhorst's *Kryptogamenflora.* Bd. X, Dritte Abteilung, 1 Teil, 2 Teil, Leipzig.

SCHLENZKA, KAPT., 1913. *Wissenschaftliche Forschungen auf der Ausreise S.M.S. 'Möwe' nach Südwestafrikas im Jahre 1911 und Vermessungs arbeiten an der Küste des deutschen Schutzgebietes.* Ann. Hydrogr. Berl. J. XLI, pp. 1–20.

SCHNAKENBECK, W., 1930. *Ueber die Ursachen der grossen Fischsterben an der Südwestafrikanischen Küste.* Fischerböte, vol. XXII, pp. 408–10.

SCHOTT, G., 1902. *Die Auftriebzone an der Kuste von Südwestafrikas.* Wiss. Ergebn. 'Valdivia', Bd. I, p. 124 *et seq.*

—— 1931. *Der Peru-Ström und seine nordliche Nachbargebiete in normaler und anormaler Ausbildung.* Ann. Hydrogr. Berl. J. LIX, pp. 161–9, 200–13, 240–52.

—— 1932. *The Humboldt current in relation to land and sea conditions on the Peruvian coast.* Geography, vol. XVII, pp. 87–98.

—— 1942. *Geographie des Atlantischen Ozeans,* 438 pp. C. Boysen, Hamburg.

—— 1951. *Der Peru Ström.* Erdkünde, Bd. V, pp. 316–19.

SCHOTT, G., SCHULTZ, B. and PERLEWITZ, P., 1914. *Forschungsreise der S.M.S. 'Möwe' in Jahre 1911.* Arch. dtsch. Seewarte, vol. XXXVII, pp. 1–104.

SCHRÖDER, B., 1900. *Das Phytoplankton des Golfes von Neapel nebst vergleichenden Ausblicken auf das des Atlantischen Ozeans.* Mitt. zool. Sta. Neapel. vol. XIV, pp. 1–38.

SCHUBERT, K., 1951. *Das Pottwalvorkommen an der Peru Kuste.* Fischereiwelt, J. 3, Hft. 8, pp. 130–1.

SCHULZ, BRUNO, 1917. *Neue ozeanographische Untersuchungen im Auftriebsgebiete der Westküste Nord Americas.* Ann. Hydrogr. Berl. J. XLV, pp. 408–16.

SCHUMACHER, A., 1935. *Uber Stromkabbelungen besonders im Guineaström und seiner Umgebung.* Ann. Hydrogr. Berl. J. LXIII, pp. 373–82.

—— 1943. *Monatskarten der Oberflächenströmungen im äquatorialen und südlichen Atlantischen Ozean.* Ann. Hydrogr. Berl. vol. LXXI, pp. 209–19.

SCHUTT, F., 1896. *Gymnodiniaceae, Prorocentracea, Peridiniaceae, Bacillariaceae* in Engler and Prantl, *Die natürlichen Pflanzenfamilien.*, Teil I, Abt. B, pp. 1–153, Leipzig.

SCHWEIGGER, E., 1949. *Der Peru Ström nach 12 jährigen Beobachtungen.* Erdkunde, vol. III, pp. 121–32 and 229–40.

SEARS, MARY, 1954. *Notes on the Peruvian coastal current.* I. *An introduction to the ecology of Pisco Bay.* Deep Sea Res. vol. I, pp. 141–69.

SEIWELL, H. R. and SEIWELL, G. E., 1938. *The sinking of decomposing plankton in sea water and its relationship to oxygen consumption and phosphate liberation.* Proc. Amer. Phil. Soc. vol. LXXVIII, pp. 465–81.

SLABBER, M., 1778. *Natuurkundige Verlustigengen, behelzende microscopice Waarneenimgen van In-en Uitlandse, Water-end Land Dieren.* Haarlem, Basch. 166, pp. 18, T (1771).

SLEGGS, G. F., 1927. *Marine phytoplankton in the region of La Jolla, California, during the summer of 1924.* Bull. Scripps Inst. Oceanogr. Tech. Ser. I, pp. 93–117.

SMITH, WM., 1853–6. *A synopsis of the British Diatomaceae*, vol. I, 1853; vol. II, 1856. London.

SPÄRCK, R., 1951. *Density of animals on the ocean floor.* Nature, Lond. vol. CLXVIII, p. 112.

SPÄRCK, R., 1953. P. 201 in *The Galathea Deep Sea Expedition 1950–1952.* Edited by Anton F. Brunn, Sv. Greve, Hakon Mielche and Ragnar Spärck. George Allen and Unwin Ltd, London.

SPROSTON, NORA G., 1949. *A preliminary survey of the plankton of the Chu-San Region with a review of the relevant literature.* Sinensia, vol. XX, pp. 58–161.

STATION LIST, R.R.S. 'William Scoresby' 1931–38, publ. 1949. Discovery Rep. vol. XXV, pp. 143–280.

—— 1950, publ. 1953. Discovery Rep. vol. XXVI, pp. 211–58.

STEEMAN-NIELSEN, E. and JENSEN, E. AABYE, 1957. *Primary oceanic production.* Galathea Rep. Sci. Res. Dan. Deep-Sea Exped. 1950–2, vol. I, pp. 49–136.

STEUER, A. D., 1911. *Leitfaden der Planktonkunde.* Leipzig and Berlin.

STEVENSON, R. E. and GORSLINE, D. S., 1956. *A shoreward movement of cool subsurface water.* Trans. Amer. Geophys. Un. vol. XXXVII, pp. 553–7.

STIGLICH, GERMÁN, 1925. *El fenomeno maritimo del Aguaje.* Rev. Mar. Peru, vol. X, pp. 25–40.

STOCKS, T., 1941. *Grundkarte der Ozeanischen Lotungen. Blatt* SII_1. Wiss. Ergebn. dtsch. atlant. Exped. 'Meteor', Bd. III, Teil I, Lief. 4.

STRØM, K. M., 1936. *Land locked waters. Hydrography and bottom deposits in badly ventilated Norwegian fjords with remarks upon sedimentation under anaerobic conditions.* Norsk. Vidensk. Akad. I. Mat. Naturv. Klasse, no. 7, 85 pp.

—— 1939. *Land-locked waters and the deposition of black muds*, in P. D. Trask: *Recent marine sediments*, pp. 356–72. London.

SUBRAHMANYAN, R., 1946. *A systematic account of the marine plankton diatoms of the Madras coast.* Proc. Ind. Acad. Sci. vol. XXIV, no. 4, Sec. B.

SUPAN, A., 1891. *Das Kalte Auftriebwasser.* Petermanns geogr. Mitt. vol. XXXVII, p. 293.

SURIRAY MSS. LAMARCK, 1816. (1836) ex PRATJE, A., 1921. Noctiluca miliaris *Suriray. Beitr. z. Morphologie, Physiologie u. Cytologie.* I. *Morph. u. Phys.* Arch. Protistenk. vol. XLII, no. I.

SVERDRUP, H. U., 1938. *On the process of upwelling.* J. Mar. Res. vol. I, pp. 155–64.

SVERDRUP, H. U. and FLEMING, R. H., 1941. *The waters off the coast of Southern California, March to July, 1937.* Bull. Scripps Instn Oceanogr. vol. IV, pp. 261–378.

SVERDRUP, H. U., JOHNSON, MARTIN W. and FLEMING, R. H., 1946. *The Oceans.* Prentice Hall Inc., New York.

TAKANO, HIDEAKI, 1954. *Preliminary report on the marine diatoms from Hachijô Island, Japan.* Bull. Jap. Soc. Sci. Fish. vol. XIX, no. 12.

TATTERSALL, OLIVE S., 1955. *Mysidacea.* Discovery Rep. vol. XXVIII, pp. 1–190.

THORADE, H., 1909. *Über die Kalifornische meeresströmung.* Ann. Hydrogr. Berl. J. XXXVII, pp. 17–34 and 63–76.

—— 1914. *Die Geschwindigkeit von Triftströms, und die Ekmanische Theorie.* Ann. Hydrogr. Berl. J. XLII, pp. 379–91.

—— 1937. *Die Stratosphäre und Troposphäre des Atlantischen Ozean.* Ann. Hydrogr. Berl. J. LXV, pp. 174–84.

TOYNBEE, H., 1883. *Die physische Ozeanographie der Kap der Gut Hoffnung usw.* Ann. Hydrogr. Berl. J. XI, pp. 1–5, 63–9, 199–205 and 331–7.

TOWNSEND, C. H., 1925. *The distribution of certain whales as shown by log-book records of American whaleships.* Zoologica, N.Y. vol. XIX, pp. 1–50, maps I–IV.

WALDRON, F. W., 1901. *On the appearance and disappearance of a mud island at Walfisch Bay.* Trans. S. Afr. Phil. Soc. vol. XI, pp. 185–8.

WALLICH, G. C., 1860. *On the siliceous organisms found in the digestive organs of the Salpae.* J. R. Micr. Soc. vol. VIII, pp. 147–53.

WALTHER, H., 1893. *Von Kapstadt nach Loanda.* Ann. Hydrogr. Berl. J. XXI, pp. 435–7.

WATTENBERG, H., 1928. *Die Phosphat und Nitrat untersuchungen der Deutschen Atl. Exped. auf dem 'Meteor'.* Rapp. Cons. Explor. Mer. vol. LIII, pp. 90–4.

—— 1933. *Das chemische Beobachtungsmaterial und seine Gewinnung.* Wiss. Ergebn. dtsch. atlant. Exped. 'Meteor', Bd. VIII.

—— 1938 *et seq. Die Verteilung des Sauerstoffs und des Phosphats im Atlantischen Ozean.* Wiss. Ergebn. dtsch. atlant. Exped. 'Meteor', Bd. IX.

WHIPPLE, GEORGE CHANDLER, 1908. *The microscopy of drinking-water.* 2nd ed. John Wiley and Sons, New York.

WILLIAMS, C. B., 1947. *The logarithmic series and its application to biological problems.* J. Ecol. vol. XXXIV, no. 2, pp. 253–72

WIMPENNY, R. S., 1936. *The size of diatoms.* I. *The diameter variation of* Rhizosolenia styliformis *and* Rh. alata *in particular and of pelagic marine diatoms in general.* J. Mar. Biol. Ass. U.K. vol. XXI, no. 1.

WITTE, E., 1880. *Das Emporquellen von kalten wasser an meridional Küsten.* Ann. Hydrogr. Berl. J. VIII, p. 192.

—— 1900. *Das Kalte Küstenwasser.* Ann. Hydrogr. Berl. J. XXVIII, pp. 74–5.

WÜST, G., 1935. *Die Stratosphäre des Atlantischen Ozeans.* Wiss. Ergebn. dtsch. atlant. Exped. 'Meteor', vol. VI, Teil 1, Lief. 2.

—— 1950. *Blockdiagramme des Atlantischen Zirkulation auf grund des 'Meteor' ergebnisse.* Kieler Meeresforsch. Bd. VII, Hft. 1.

YOSHIDA, K., 1955. *Coastal upwelling off California.* Rec. Oceanogr. Wks Jap. vol. II, no. 2.

YOSHIDA, K. and MAO HAN-LEE, 1957. *A theory of upwelling of large horizontal extent.* J. Mar. Res. vol. XVI (1), pp. 40–54.

ZOBELL, C. E. and RITTENBERG, S. C., 1948. *Sulfate reducing bacteria in marine sediments.* J. Mar. Res. vol. VII, no. 3, pp. 602–17.

ZORRELL, F., 1928. *Der 'El Nino' Ström im Jahre 1925.* Ann. Hydrogr. Berl. J. LVI, pp. 166–75, also 1931, pp. 161, 200 and 240.